JOURNAL OF AGRICULTURAL RESEARCH

VOL. 57 WASHINGTON, D. C., AUGUST 15, 1938 No. 4

RATE OF SPREAD OF SURFACE FIRES IN THE PONDEROSA PINE TYPE OF CALIFORNIA[1]

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INTRODUCTION

Studies of forest-fire behavior have as their broad objective the determination of the natural laws governing primary ignition and subsequent rate of spread of fires in forests and in related types of inflammable vegetation. The purpose of such studies is to provide an improved foundation for fire control, a major activity in American forestry. Scientific evaluation of the factors affecting fire behavior cannot replace experience gained in fire-control operations. Such research can, however, supplement experience by providing information not obtainable on the fire line and, by explaining observed fire phenomena, make them more understandable and predictable. Fire-behavior studies are needed to give information essential to the extension of methods of forecasting fire danger, to permit determination of size-of-crew and speed-of-attack requirements, and, finally, to promote development of fire-suppression tactics and strategy.

Gisborne (*3*),[3] Stickel (*9*), Nichols,[4] and others have studied forest-fire ignition hazard through the determination of variations in fuel-moisture content under varying weather conditions, relating these moisture variations to ignitibility through tests with various firebrands. Through the work of these investigators we know that with ordinary firebrands—as matches, smoking materials, and small campfires—ignition occurs only when the forest fuels contain moisture amounting to less than 30 percent of the dry weight of the fuel. These studies have also resulted in an understanding of the influence of meteorological factors on moisture variations in the fuel, permitting estimation of moisture from a knowledge of weather factors.

Show (*6*) first studied rate of spread in 1916 and 1917, using small test fires. As a result of observations made on 33 fires during this period, he concluded that fires burning under conditions favorable to rapid spread tend to burn with acceleration, while slower-burning fires tend to burn at a steady rate. His observations also led him to conclude that the effect of wind could be expressed as a function of the square of the wind velocity. Through theoretical analyses of the factors influencing combustion in the open, Hawley (*4*) and Gray[5] have contributed in a major way to the advancement of fire-behavior knowledge. Show and Kotok, in analyzing the California fire records, have broadly defined the influence of cover type (*8*) and

[1] Received for publication December 15, 1937; issued August 1938.

[2] Maintained in cooperation with the University of California at Berkeley, Calif.

[3] Italic numbers in parentheses refer to Literature Cited, p. 267.

[4] NICHOLS, L. H. THE BURNING OF SETTLERS' SLASH AND METEOROLOGICAL CONDITIONS IN THE PROVINCE OF QUEBEC DURING 1931. Quebec Forest Indus. Assoc., Ltd. Rept. 4, 22 pp., illus. 1931. [Mimeographed.]

[5] GRAY, L. G. PRELIMINARY REPORT ON FIRE HAZARD RATING STUDY. U. S. Weather Bur., 54 pp., illus. San Francisco. [Mimeographed.]

weather factors (7) on rate of spread. These studies have resulted in determination of the speed of attack required for effective suppression under hazardous conditions.

The present study may be considered a continuation of the work begun by Show in 1916. The primary purpose of both studies was the exploration and definition of the relationships between fuel, fuel moisture, weather factors, and rate of spread. Pure stands of ponderosa pine (*Pinus ponderosa* Dougl.) were chosen for these experiments because it was the simplest fuel type available and because it is an extensive and commercially important timber type. By initiating studies in a simple type, it was considered probable that relationships would be developed of value to the extension of rate-of-speed information to other more complex types.

DETAILS OF STUDY

SELECTION OF VARIABLES

Studies of fire behavior are made complex (1) by the number of factors involved and (2) by the variation found in these factors from place to place and from time to time within the forest. Wind normally fluctuates widely both in intensity and direction, and this characteristic is intensified in the forest by the resistance offered by the foliage and tree trunks. Fuels in themselves vary widely from place to place within the stand, and the moisture content of fuels is constantly changing with changes in weather conditions.

Six primary factors are recognized in rate-of-spread studies, viz: (1) Fuel size and arrangement; (2) moisture content of the fuel; (3) air supply (wind movement); (4) slope of the ground; (5) the tendency of fires to burn at an increasing rate, or the effect of time; and (6) size of the fire. The first five factors listed are independent variables while the sixth is the variable under study, or the dependent variable. Although other important variables may be defined by further research as affecting fire spread, the problem may at this stage be considered essentially one of relating rate of increase in fire size to concurrent variations in the five other variables listed.

Present knowledge of the factors influencing combustion in the open contains no information on methods of measuring one factor, variation in the physical characteristics of forest fuels. Hawley (4) has suggested the use of the surface-volume ratio as an approach, but the specific technique of measuring this, or any other fuel factor which might be used to explain rate-of-spread fluctuations, remains to be developed. This lack of a well-defined theory and technique for the measurement of the fuel variable made it necessary in the present study to eliminate this factor so far as possible. This was the primary reason for the selection of the ponderosa pine type, which contains the most uniform fuel conditions to be found in California. Under some situations in this type, usually in dense even-aged stands, the fuels present consist almost entirely of a layer of pine needles from 1 to 4 inches in thickness.

SELECTION OF SITES

Characteristic virgin stands of ponderosa pine were not suitable as sites for this study. They consist of groups of mature and overmature trees interspersed with more open areas occupied with brush,

or reproduction of various ages. Litter accumulates to depths of 4 to 5 inches within the dense groups, while a few feet away, in an opening between groups, the ground may be bare. Such fuel conditions were too uneven to meet the study specifications.

Only two kinds of stand within the type were found with sufficiently uniform surface fuel. Optimum conditions were found within certain even-aged dense stands of ponderosa pine on the Shasta Experimental Forest, usually 45 to 50 years of age, and averaging about 600 trees to the acre, with an average diameter breast high of 9 inches, and a height of 60 feet. Certain uniform, relatively dense even-aged virgin stands in which the younger trees had been killed by light fires were also well adapted to the study. The generalizations made in this report as to surface fires in the ponderosa pine type should therefore be applied specifically only where the fuel conditions are uniform; that is, where the ground is completely covered by at least 1 inch of pine needles.

Fortunately for the simplification of the first year's study, the second-growth stands on the Shasta Experimental Forest occurred on level ground, permitting the elimination of slope as a variable and reducing the number of variables to be measured to four, viz: (1) Size of fire; (2) moisture of fuel; (3) wind velocity; and (4) effect of time. In all, tests were conducted on 13 carefully selected sites during the first year's study. During 1934, the fires were confined to two sites and included studies of fires on sloping ground.

CONDUCT OF TESTS

The primary factors measured on each fire were fuel moisture, wind velocity, perimeter at each 2-minute interval, and, where important, slope. In addition, several secondary factors were recorded, as depth of litter, air temperature, surface-fuel temperature, relative humidity, and barometric pressure.

For the plotting of perimeter, steel stakes were set at 5-foot intervals on lines radiating from the central ignition point. With these stakes in place it was practical for the plotter to enter the perimeter of the fires directly on polar coordinate paper. Figure 1 illustrates a fire 8 minutes after ignition on a typical test plot. Plotting was ordinarily done on a sketching tripod, as shown.

Samples for moisture-content determinations were gathered immediately before the start of the fire. Two methods were used at different times during the tests. The first consisted of gathering two samples, one in an open exposed part of the test plot, and a second in a more dense, covered portion. By the second method a single sample was taken of the top needles over the whole plot. Because rather wide variations were found over the plots, the average moisture value obtained by the second method proved the most useful. Samples were collected in friction-lid cans and were weighed the day of collection. Because of lack of facilities in the field, all moisture determinations were made at one time, at the end of the field season. The initial moisture determinations were based on ordinary oven-drying procedure. Later, studies by Buck (*1*) led to the use of a more accurate and speedy xylene distillation method. Moisture percentages used in this report have all been reduced to the xylene

distillation standard, which is about 1.5 percent higher in indicated moisture content than originally computed on an oven-dry basis.

The measurement of wind velocities on the test fires presented problems in the selection of an instrument and in the choice of height above ground surface at which the measurement would best represent the influence of wind on rate of spread. Wind velocities within closed stands are relatively light in comparison with concurrent velocities in the open, but nevertheless have a great influence on rate of spread. The ordinary three-cup anemometer was found to lack the sensitivity required for measuring these light winds. The Biram type (fig. 2) is much more sensitive and was used on all fires studied. To adapt this anemometer to the study of test fires, it was mounted on bearings, and provided with a vane to maintain its axis parallel to the wind

FIGURE 1.—Test fire in typical even-aged stand of ponderosa pine 8 minutes after ignition. The uniform nature of the fuel is characteristic of the locations sought in these experiments.

direction. So adapted, this type is recommended for all similar studies. An anemometer on the hot-wire principle was tried later, but produced records no more useful than those obtained with the Biram type. After some experimentation, 30 inches above ground surface was selected as the desirable standard height for measurement of wind velocities, and throughout the study the anemometers were so mounted. Although an automatic recorder was developed toward the end of the experiment, the data used in the analysis consisted entirely of velocities recorded visually each 30-second interval over the period of the tests.

Time records were taken with stop watches from the instant the match was applied. On a portion of the fires, temperatures attained by the fire during combustion were measured with thermocouples. Records of air temperatures, litter temperature, relative humidity, and barometric pressure were obtained with standard instruments. A detailed description, including needle depth, crown density, open-

ings in the canopy, and size of trees, was made for each plot. A running description of the behavior of each fire was a part of the routine observations.

On the smaller fires, one man plotted perimeter, a second recorded wind movement, while a third made a running description of the fire. On the larger fires the number of men was increased to a maximum of seven, to allow more men for recording wind velocity, plotting perimeter, and operating the thermocouple apparatus.

FIGURE 2.—Biram (vane) type anemometer mounted on a special tripod and fitted with a large direction vane.

In the test-fire procedure, after the selection of the test plot by the chief of party, a crew set the lines of stakes, using compass and tape, and taking care to disturb as little as possible the natural condition of the surface litter. While this work was proceeding another crew removed from the plot all large limbs and other debris which might influence the spread, and trimmed low dead branches which might tend to make the fire crown. In the early experiments, fire lines were cleaned around the test plots, but this practice was later abandoned, since the lines were seldom used, their preparation required considerable time, and their use reduced the number of plots that could be studied on any one site.

During the process of plot preparation, the plot description was made, emphasizing any abnormal or unusual features; record forms were prepared; and the anemometer was set up to windward within 10 feet of the estimated reach of the fire line. Thermometers were exposed in the litter, to be read just prior to the start of the fire.

Fire-fighting equipment was then assembled, water supplies inspected, and the suppression crew distributed. At this point a check on the progress of all preparations made it possible to set a time for the start of the fire. The final records, temperature, humidity, and

litter moisture were taken within a 5-minute period preceding the starting time.

The fire was started by applying a single match at the center stake and simultaneously the stop watches of the observers were started. Thereafter all records of wind, perimeter, and fire behavior were maintained according to stop-watch readings. Perimeter was recorded on the smaller fires at each even 2-minute period. On larger fires it was found desirable for the plotter to travel continuously around the fire, marking the perimeter location and the time of observation to the second. The accumulated total wind movement was read at each 30-second interval.

At the conclusion of the test, the fires were stopped by the application of water. With the edge of the fire dead, the smoldering litter was systematically extinguished to the center. By fast, thorough action it was usually possible to extinguish a test fire completely and to clear a fire line to mineral soil around it within 20 minutes of the end of the study. With experience, it was possible to obtain from two to five tests a day, depending on the area of the fires. Test plots were inspected regularly for several days following the fire.

During the 1933 field season, 95 selected test fires were studied on the Shasta Experimental Forest, under uniform conditions in the ponderosa pine type. During this season, the fires were allowed to attain a size of one-sixtieth to one-fortieth of an acre, the maximum size readily extinguishable with the facilities available. The period of study was ordinarily 18 minutes, although some slow-burning fires were allowed to spread for 30 minutes or more. Extremely rapid-burning fires were, for reasons of safety, suppressed at 12 or 14 minutes.

Preliminary analysis of the 1933 records showed that the data could be much improved through additional studies over a longer total burning period. Some data on the effect of slope were also desired. In 1934 an area in ponderosa pine was selected on the Lassen National Forest, 100 miles south of the 1933 center of work, and here 69 fires were set, 46 of these being on slopes above 10 percent in grade. During this second season, the tests ran for 30 minutes on the 23 fires on level ground. These fires attained areas of 0.05 to 0.5 acre. The suppression problem was increased to an extent sufficient to reduce materially the number of fires studied.

GENERAL CHARACTERISTICS OF THE DATA

A cursory examination of the data available at the completion of the tests revealed large fluctuations in rate of spread at different hours of the day. A fire at 7 a. m. might reach a perimeter of 25 feet in a 12-minute period and later, on the same day, another might attain 150 feet during the same burning period. Even average values fluctuated widely with time of day, as shown in table 1.

The summer climate of northeastern California is remarkably uniform. During the period of these tests, little or no precipitation occurred and clouds were uncommon. Minimum temperatures at night ranged from 30° to 55° F., while maximum day temperatures were within a range of 70° to 90°. Relative humidities in the summer at this elevation (4,000–5,000 feet) vary from 100 percent in the early morning hours to a minimum of 10 to 11 percent in the early afternoon.

TABLE 1.—*Hourly averages of rate-of-spread factors of fires, 1933–34*

Hour of day	Fires	Area in 12 minutes	Perimeter in 12 minutes	Wind velocity per hour	Moisture content	Relative humidity	Air temperature
A. M.:	*Number*	*Square feet*	*Feet*	*Miles*	*Percent*	*Percent*	*° F.*
7	1	60	30	0.0	12.5	45.0	72.0
8	6	95	36	.3	10.0	60.8	58.7
9	12	164	44	.9	9.9	42.9	66.9
10	21	285	62	2.1	9.1	31.8	73.7
11	14	320	66	1.7	8.6	28.4	75.5
12	2	295	64	1.2	7.6	22.5	83.0
P. M.:							
1	14	476	84	2.0	7.0	22.2	83.2
2	17	458	80	2.0	6.6	22.9	81.4
3	11	328	67	1.3	7.1	22.8	81.9
4	11	257	60	1.1	6.8	23.3	82.5
5	3	212	54	.6	6.9	31.7	78.3
6	2	104	38	.0	8.0	48.5	68.0
7	1	133	42	.5	8.3	53.0	68.0
8	2	166	48	.8	9.0	54.5	66.5

One striking fact illustrated by table 1 is the average low wind velocity recorded on these fires. From this it might be inferred that the tests were conducted purposely at times of light wind. In fact, however, windy conditions were sought rather than otherwise, but velocities within the stands were seldom greater than 3.5 miles per hour and then only for short periods. This was due to high efficiency of the timber as a windbreak. It can be stated as a result of these observations, and on the strength of further studies by the authors, that winds near the ground in moderately dense stands seldom attain a velocity greater than 3 miles an hour even when in the open they reach 30 or more miles an hour.

The tendency illustrated in the table for high wind velocity and low moisture content to occur during the same periods was noted in conducting the tests. Wind in the area where the tests were located is largely controlled by thermal convection, with the strongest movement during that part of the day when air temperature is highest. Absolute humidity tending to remain constant, the moisture content of light fuels in the areas studied responded quickly to changes in temperature. While this phenomenon is undoubtedly characteristic of other forests, it is particularly pronounced in the summer climate of interior California where air conditions are characteristically stable.

The average moisture content of litter shown in table 1 ranges from 6.6 to 12.5. The total range on these plots was from 4.0 to 13.5 percent. Since all fires were studied during a period when rain had not fallen for several weeks, it may be assumed that these variations are the result of diurnal fluctuations in atmospheric conditions.

Figure 3 illustrates characteristic types of perimeter records. The lines on the chart represent the margin between flames and unburned litter at successive 2-minute intervals. On the slower fires the width of the flaming area was about 6 inches, but on fast fires the flames might attain on the leeward side a width of several feet.

The simplest type of fire is that shown in figure 3, *A*, where air movement is too light to affect spread appreciably. Such a fire soon develops into a thin ring of fire with the flames turning inward and upward as shown in figure 1. This tendency of flames to burn inward

is due to the displacement of the hot gases rising from the smoldering interior by cool air from outside the ring of fire. In the absence of changes in fuel conditions, fuel moisture, and wind, the rate of spread of such a fire would vary only during the period when the fire was becoming established, and with changes in the indraft due to variations in the volume of rising gases. The regularity shown in the burning rates of fires of this type gave support to the assumption of uniform fuel conditions.

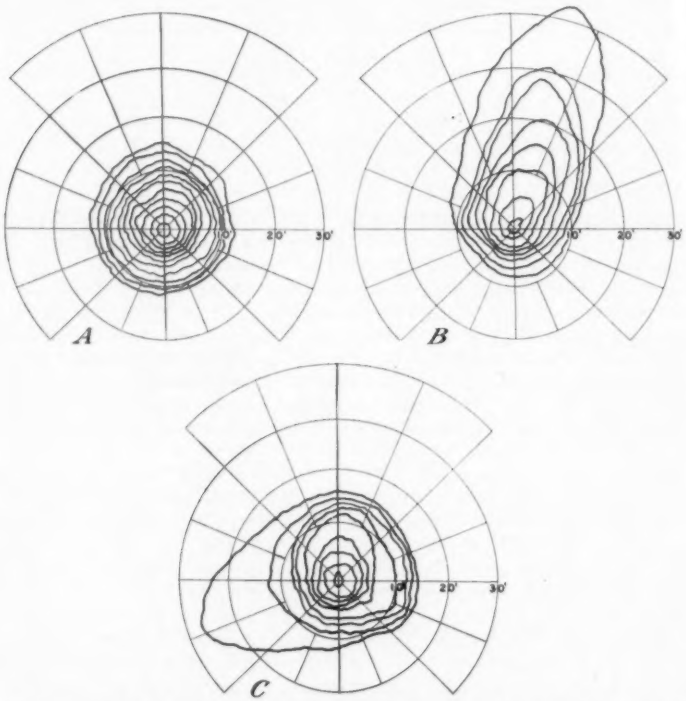

FIGURE 3.—*A*, Diagram of slowly spreading fire: Average wind velocity 0.2 mile per hour, fuel moisture content, 7.0 percent; perimeter shown at each 2-minute interval. *B*, Diagram of rapidly spreading fire with constant wind direction: Average wind velocity 2.0 miles per hour; fuel-moisture content 4.3 percent; perimeter shown at each 2-minute interval. *C*, Diagram of rapidly spreading fire with variable wind direction: Average wind velocity 1.1 miles per hour; fuel moisture-content 9.0 percent; perimeter shown at each 2-minute interval.

The chart of a fire burning under a wind of constant direction and under comparatively uniform velocity is shown in figure 3, *B*. Although fires starting under these conditions are at first not greatly affected by the wind, they spread much more rapidly after becoming established. The shape of the fire and the rate of spread are in this case very noticeably affected by a wind of an average velocity of 2 miles per hour.

With a wind of more than 1 mile per hour, the influence on the size and shape of the flames is immediately noticeable. Flames on the

leeward side increase in size and turn outward, becoming with higher velocities approximately parallel with the surface of the ground. On the windward side, the flames are reduced in intensity and driven toward the burned area. On the flames burning at right angles to its direction, the wind has apparently little effect.

Figure 3, *C* illustrates a type of fire more characteristic of normal conditions than those shown in the two preceding charts. In this case the wind movement varied both in rate and direction. Fires behaving in this manner increase their area more rapidly than fires burning with a comparable velocity in one direction only. The effect on perimeter of such variation is, however, unimportant.

METHOD OF ANALYSIS

The first step in the analysis of the fire records consisted of measuring the perimeter increase from charts such as those shown in figure 3. Perimeter was obtained with a map measurer and checked to the nearest foot. These data, together with the corresponding data for wind velocity, moisture content, and time for the 118 fires on level ground, were then entered on 1,153 cards, each containing the complete record of one 2-minute interval. Because of the scarcity of data in the higher time classes, all cases above 22 minutes were eliminated. The reason that perimeter and not area was used is that the area of a circle, or an ellipse, increases in proportion to the square of its radius, while the perimeter increases in direct proportion to the radial increase. The rate at which the area of a fire increases is, consequently a function of the size of the fire, while the rate of perimeter increase is, geometrically speaking, independent of size. Furthermore, perimeter is of greater significance in fire control, as better representing the suppression effort required.

The Pearsonian mathematical method of multiple linear correlation was first considered. Two difficulties presented themselves, however: (1) The relationships so derived would be linear, whereas it was considered probable that the relationships were in part curvilinear; (2) this form of analysis is unsuited to definition of relationships where joint correlation exists; that is, where the influence of any one independent variable on the dependent variable is affected by the size of another independent variable. Show (*6*) discovered the presence of joint correlation in his 1916 data and preliminary curves in the present analysis confirmed this finding. Consequently, methods which would permit the definition of joint correlation, if it existed, were desirable. These considerations led to the use of methods recommended by Ezekiel (*2*) for problems of joint correlation. Inasmuch as these methods enter into discussion of the analyses finally developed, they are explained in detail.

First, all cards were sorted into 2-minute time groups. Next, the cards in each time class were sorted into three moisture classes—below 7.4 percent, 7.5–10.4, and 10.5 and more. A third segregation was then made within each moisture class, on wind velocity, five wind-velocity classes being recognized as follows: 0.0–0.9 miles per hour, 1.0–1.9, 2.0–2.9, 3.0–3.9, and 4.0+. Eleven tables of the type shown in table 2 resulted, one for each 2-minute period.

TABLE 2.—*Summary of values of wind velocity, moisture content, and perimeter for first 2-minute periods,*[1] *on a basis of 118 fires on level ground*

FOR CLASS VALUE X_3=0.0–7.4

Class value X_2	N	Total X_1	Mean X_1	Total X_2	Mean X_2	Total X_3	Mean X_3
0.0–0.9	12	94	7.8	8.7	0.7	79.2	6.6
1.0–1.9	23	203	8.8	31.7	1.4	147.2	6.4
2.0–2.9	5	43	8.6	11.5	2.3	29.0	5.8
3.0–3.9	4	44	11.0	14.3	3.6	22.8	5.7
4.0+	4	42	10.5	19.0	4.8	25.2	6.3

FOR CLASS VALUE X_3=7.5–10.4

0.0–0.9	23	147	6.4	9.3	0.4	202.4	8.8
1.0–1.9	20	137	6.8	26.7	1.3	182.0	9.1
2.0–2.9	11	81	7.4	26.8	2.4	93.5	8.5
3.0–3.9	1	8	8.0	3.2	3.2	7.8	7.8
4.0+	3	25	8.3	13.1	4.4	26.1	8.7

FOR CLASS VALUE X_3=10.5+

0.0–0.9	9	46	5.1	1.5	0.2	99.0	11.0
1.0–1.9	2	9	4.5	2.3	1.2	21.6	10.8
2.0–2.9							
3.0–3.9	1	5	5.0	3.3	3.3	11.0	11.0
4.0+							

[1] X_1=Perimeter increase in feet per 2 minutes; X_2=wind velocity in miles per hour, average during 2-minute period; X_3=moisture content in percent, based on xylene distillation method; N=number of cases.

The next step was to plot the average value of the dependent variable (perimeter increase) on the average values of wind as a first approximation of the influence of that variable. Wind was used in the first approximation because preliminary studies had shown its influence to be most strongly defined. Three curves showing the effect of wind on perimeter increase, one for each moisture class, were constructed freehand for each time interval, a total of 33 curves in all. These curves served as a first approximation of the influence of wind velocity on perimeter increase throughout the entire range of moisture and time conditions.

To determine the influence of moisture, a second series of approximation curves was drawn, using the first curves as a base, with moisture content plotted on the horizontal axis. After these plotted points were smoothed by freehand, a third approximation was made with time plotted on the horizontal axis. The fourth smoothing was made with wind velocity plotted on the horizontal axis as in the first approximation. Changes in the relationships became smaller at each smoothing and were finally considered negligible after the seventh and final smoothing.

Several correlation studies of this type were made from the data. The results obtained are dependent to some degree upon the first approximation, where the personal judgment of the one analyzing the data is important. Checks on the final results were made by smoothing in one correlation first on wind and in another first on moisture. Although the variations obtained in the final curves were not great, it was desirable to find a method of analysis less subject to this type of variation.

As anticipated, joint correlation existed in the data and was particularly noticeable in the change in the slope of the curves of wind

velocity with increasing time. Some changes were also noted in the slope of the moisture curves with variations in time. On the other hand, no tendency for the slope of the moisture-perimeter curves to vary with changes in wind velocity, or vice versa, was found in any of the several correlation studies made. This and the fact that the influence of both wind and moisture were established by these studies as linear led to a slightly different type of analysis.

If joint correlation was not present between the wind and moisture factors, but only between time and these factors, it was apparent that multiple linear regressions could be obtained for each time interval, thus eliminating personal judgment in the preliminary curving process. The influence of time, a relationship known to be curvilinear, could then be determined by successive freehand smoothings. This process was followed as outlined, multiple linear regression equations being obtained for the influence of wind and moisture for each 2-minute interval.

At this stage of the analysis a further check was obtained on the presence of curvilinearity in the moisture-perimeter and wind-perimeter relationships. Using the methods outlined by Mills (*5*), it was determined that no significant tendencies toward curvilinearity existed in any of the 11 correlations.

The next step in the analysis consisted in smoothing the regressions to obtain an expression of the influence of time. This was accomplished in the same manner as has been outlined in the discussion of the preliminary analyses. As a result of this procedure, a higher index of correlation and lower standard error were obtained than where freehand smoothing methods only were used. After the curves had been defined by successive smoothings an empirical formula was derived to express the curves mathematically. This formula and the method of derivation will be discussed subsequently. The analysis of the influences of slope on rate of spread, which was handled in a somewhat different manner, will also be discussed later.

GENERAL RESULTS

As an introduction to the results of the analysis, it may be well to review the theoretical aspects of combustion of wood as summarized by Hawley (*4*). The ignition temperature of dry wood is approximately 540° F. Inasmuch as the temperature of combustion is in the neighborhood of 1,500°, it is apparent that combustion of finely divided wood substance will readily proceed, once ignition is established, even in the presence of appreciable amounts of moisture in the fuel. The influence of moisture is explained by the fact that before combustion of wood can take place, all water in it must be raised to 212°, vaporized, and the vapor raised to the ignition temperature of wood, 540°. Theoretically the amount of heat produced permits combustion to the point where 5.71 parts of water are present to 1 part of wood, assuming full utilization of all heat produced in the vaporization of the moisture. From a practical standpoint, however, because of heat loss, wood will not burn even under forced draft if there are more than 2 parts of water to 1 part of wood. Under forest conditions, only a small proportion of the total heat of combustion will be available for this purpose. Any considerable moisture content in forest fuels thus slows down combustion, through decreasing the amount of heat available for ignition of nearby fuels.

According to Hawley, at least 133 cubic feet of air are required to burn 1 pound of wood. This explains in part the influence of wind upon combustion. Wind also influences surface fires by forcing the flames close to the ground surface, thereby increasing radiation to the fuels.

It is common experience that once a fire is established it tends to burn more readily. It has been generally assumed that forest fires rapidly increase their rate of spread with time. In this investigation,

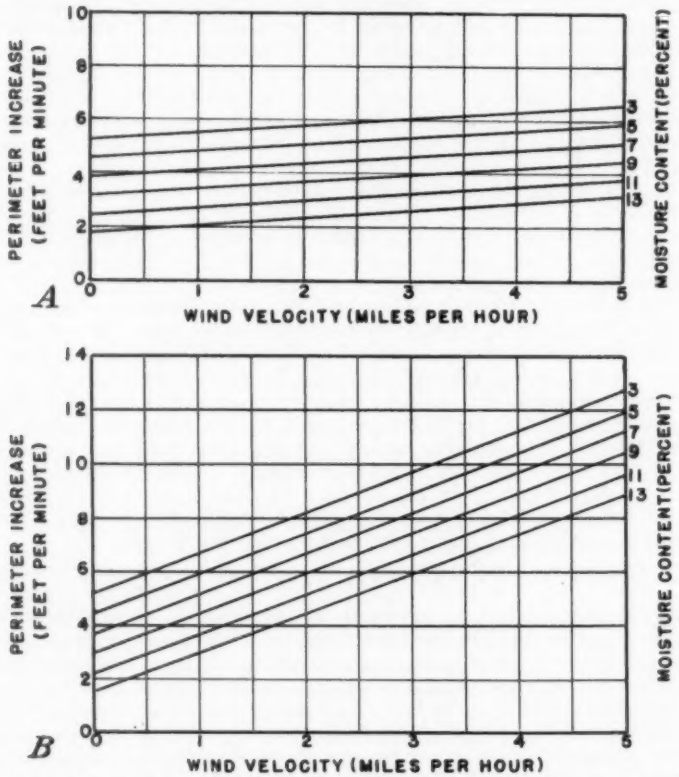

FIGURE 4.—Probable rate of perimeter increase on level ground for various wind velocities and moisture content at 2 (*A*) and at 8 (*B*) minutes from start of fire.

an attempt was made to evaluate the length of this establishment period.

In the following discussion, the effects of wind, moisture, and time are treated separately, prior to a discussion of their combined effect.

THE EFFECT OF WIND

Smoothed curves showing the effect of wind throughout the ranges of moisture and wind velocity are shown in figures 4 and 5. The representation of the influence of wind as linear is in disagreement

with the conclusions of Show (*6*). These earlier conclusions are apparently explained by the fact that it was impossible, with the limited data available in the earlier study, to separate the influence of moisture from the influence of wind. The presence of intercorrela-

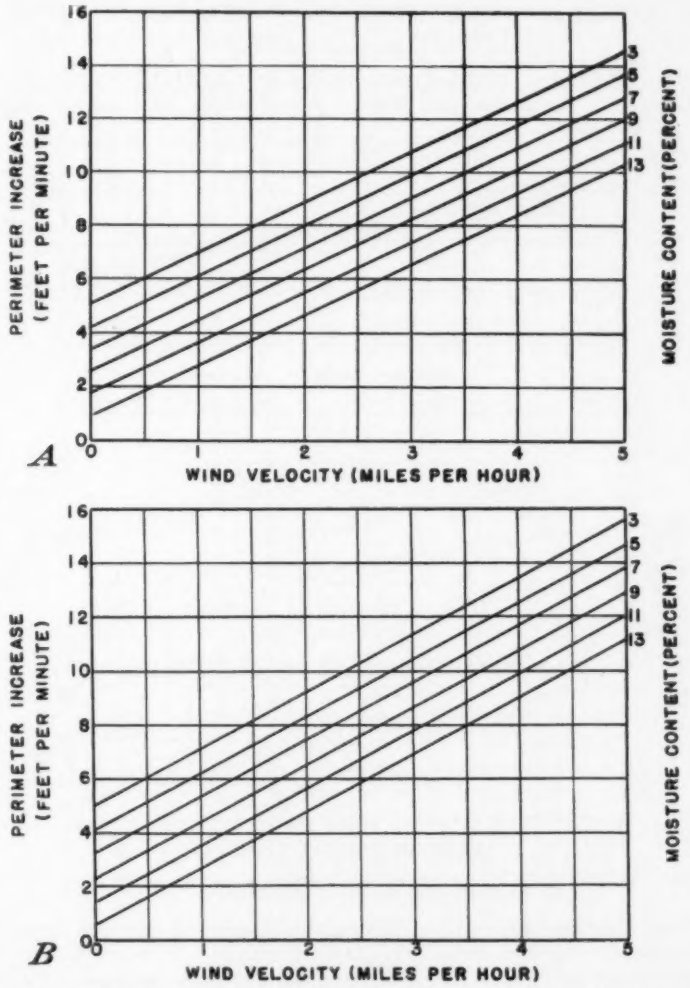

FIGURE 5.—Probable rate of perimeter increase on level ground for various wind velocities and moisture content at 14 (*A*) and at 20 (*B*) minutes from start of fire.

tion between wind and moisture was apparently not taken into account in this early work. In the present analysis, it has been possible to consider the influence of each variable within a small range of variation of the other variables.

A second characteristic of these curves deserving comment is the change of slope with increase in time. At 2 minutes, for instance, rate of spread increases about 0.3 foot with an increase of 1 mile per hour in wind velocity; at 20 minutes the increase is slightly more than 2 feet. The fact that joint correlation does not exist between moisture and wind is shown by the same slope of the lines for all moisture classes.

THE EFFECT OF MOISTURE

The influence of variations in moisture content of the litter is shown in figure 6. As in the case of wind velocity, the relationship shown

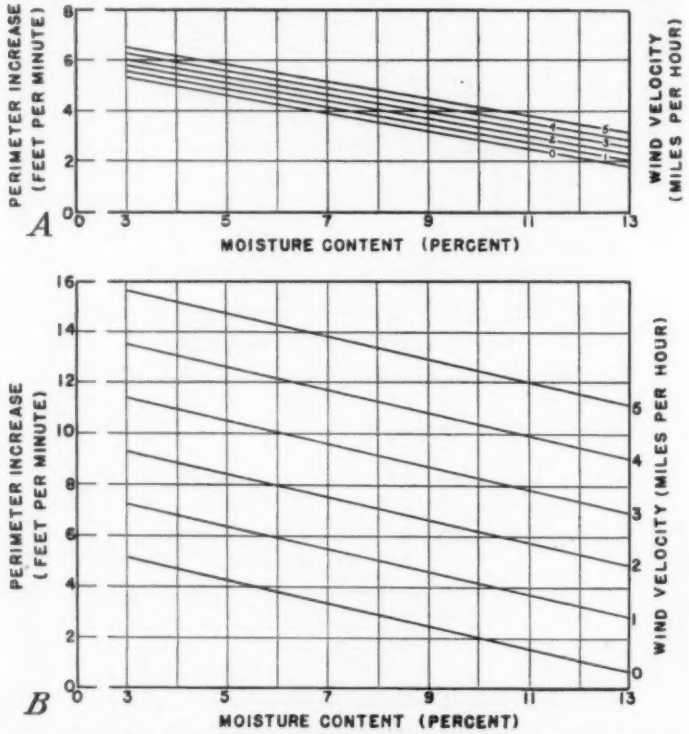

FIGURE 6.—Probable rate of perimeter increase on level ground for various values of litter moisture content and various wind velocities at 2 (*A*) and at 20 minutes (*B*).

is linear throughout the range of time since start of fire; the slope of the moisture curves is negative. Only sufficient curves are shown to illustrate the general character of the moisture-perimeter relationship.

Joint correlation between time and moisture is shown by the variation in the slope of the moisture curves with changes in time; the variations, however, are less pronounced than in the case of the perimeter-wind curves. Because of this joint correlation, it is difficult to generalize broadly on the influence of either the wind or moisture. If any one time is selected, a relative comparison of the influence of

wind and moisture content is possible. At the 20-minute time interval the influence of 1 percent variation in moisture is approximately 0.4 foot in perimeter (fig. 6, *B*). At the same period, the influence of

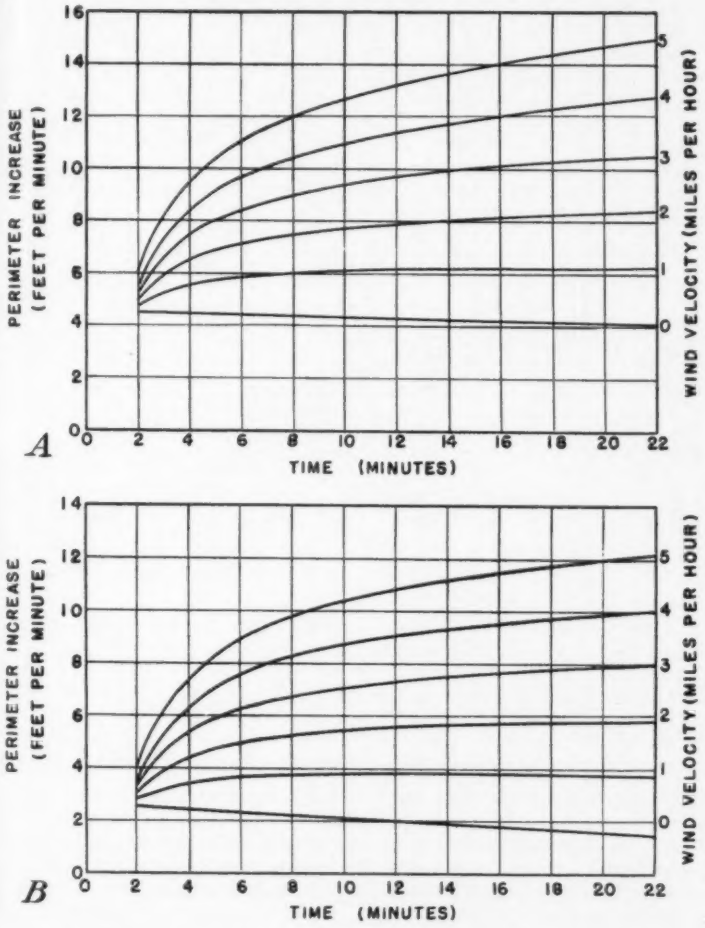

FIGURE 7.—Probable rate of perimeter increase on level ground at various times from start of fire and at various wind velocities for litter moisture content of 5 (*A*) and of 11 percent (*B*).

1 mile per hour in wind velocity is 2.0 feet (fig. 5, *B*). This ratio of 1 to 5 emphasizes the importance, as defined in this study, of wind on rate of spread, once a fire is started. In making this or similar comparisons, it should be remembered that the wind velocities shown are those measured within the stand, and do not correspond to those measured in the open. A relatively large increase of wind velocity in the open would be required to increase velocity within the stand from 3 to 4 miles per hour.

THE EFFECT OF TIME

The effect of time on rate of spread, or, as it might be expressed, the tendency of small fires to accelerate their rate of spread under various moisture and wind conditions, is illustrated in figure 7. Curves are shown for two moisture classes only—5 and 11 percent. It will be noted that, under low wind, fires tend to assume a constant rate of perimeter increase after the first few minutes of burning. With higher winds, the length of the period over which acceleration occurs increases and at the higher velocities the increase is still appreciable at 22 minutes. Presumably, however, under constant wind and moisture conditions, surface fires of this type would tend at the end of one-half hour or slightly more to burn at a steady or only slightly increasing rate.

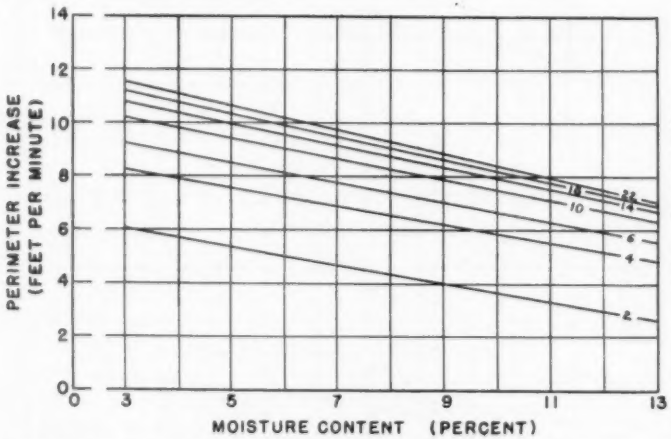

FIGURE 8.—Probable rate of perimeter increase on level ground for various values of litter moisture content and time from start of fire with wind velocity at 3 miles per hour.

COMBINED INFLUENCE OF WIND, MOISTURE, AND TIME

Consideration of the manner in which the three variables—wind, moisture, and time—act in combination to produce various rates of spread is made complex by the presence of joint correlation between time and the other independent variables. In general, it may be said that the influence of both moisture content and wind are direct, i. e., linear; and that a variation of 1 percent in moisture will influence the rate of spread by 0.4 foot per minute, while a change of wind velocity of 1 mile per hour will result in a variation in perimeter of about 2 feet per minute. These values are attained, however, only after the fire has burned for some time and they are not constant but vary with the period during which the fire has been burning. Apparently fires tend to reach a constant perimeter increase under unchanging moisture and wind conditions, but the time when this occurs cannot be closely defined from this study. It would appear, however, that the effect of time would be removed in most cases after 30 to 45 minutes. Figures 8 and 9 have been constructed to

show the variation in the effect of wind and moisture with time for the span of these tests.

Figure 10 is a drawing of a model constructed to show these relationships simultaneously. In this model, lines cutting through the diagram define the rate of spread values for various values of wind and moisture at a given time period.

The combined influence of wind, moisture, and time on rate of perimeter increase may be more definitely expressed in mathematical terms. From figures 4, *A*, and 6, *A*, and 4, *B*, and 6, *B*, it is obvious that the relationships between perimeter, wind, and moisture for any

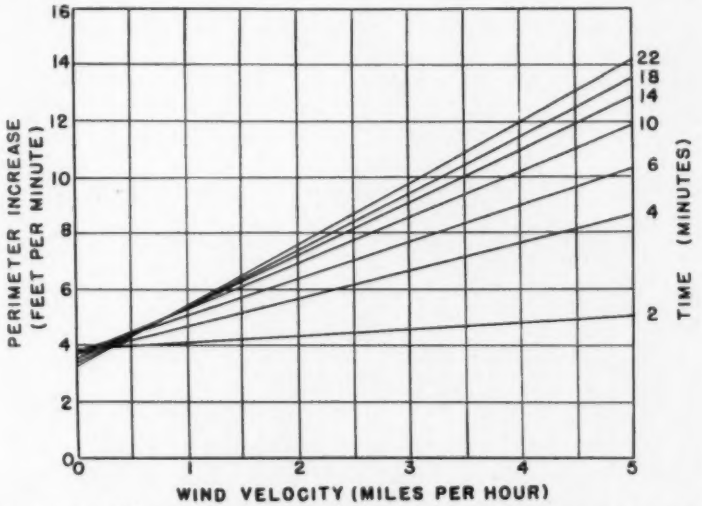

FIGURE 9.—Probable rate of perimeter increase on level ground at various times from start of fire and at various wind velocities, for litter moisture content of 7 percent.

particular time interval, as 2 minutes, may be expressed by a linear equation of the form

$$p=k-k' M+k'' V \qquad (1)$$

in which

p=rate of perimeter increase in feet per minute
V=wind velocity in miles per hour
M=moisture content in percent

The use of the minus sign with the moisture factor is explained by the slope of the moisture-perimeter curve. If formulas are derived for each time period it will be found that the constants k' and k'' will vary as some function of time. If they could be expressed mathematically and introduced into the formula, a mathematical expression of rate of perimeter increase at any time would result.

To do this, values of k' for various times from the smoothed curves were plotted on time. The variation in k' with time is small; in theory it should become constant after a short period. Within the limit of 22 minutes, however, it is practical to treat the relationship as linear,

as shown in figure 11, *A*. An expression for k' in terms of t is readily obtainable by a linear equation in the form of $k'=a+bt$.

When the values of k'' are plotted on time as in figure 11, *B*, the curve resulting is of a more complex type. This may be expressed as a power series of the form

$$k''=a+bt+ct^2+dt^3+---mt^n$$

but would have such a large number of terms that its use would be cumbersome.

The value of the constant k may be determined by extrapolation of the smoothed curves to determine the value of p when both M and

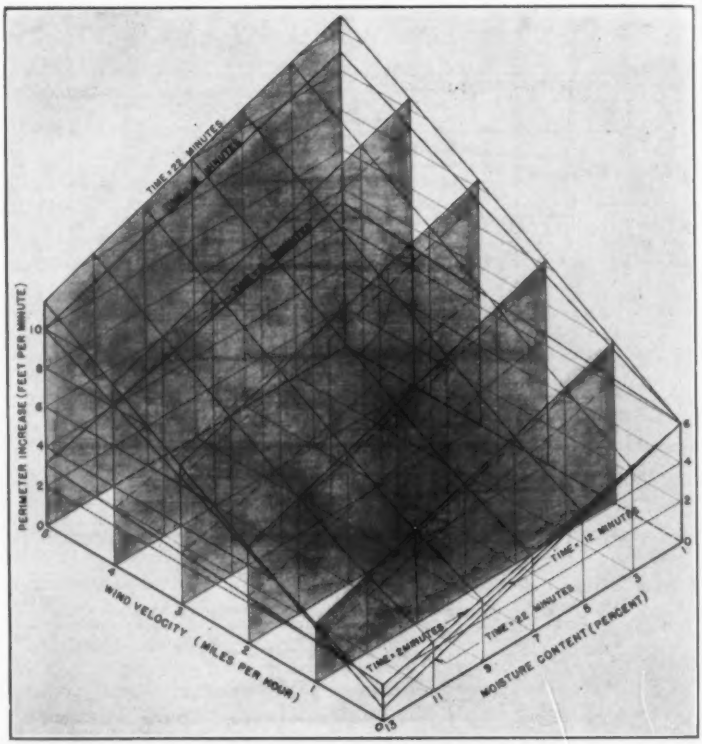
PERIMETER INCREASE (FEET PER MINUTE)
WIND VELOCITY (MILES PER HOUR)
MOISTURE CONTENT (PERCENT)
TIME = 22 MINUTES
TIME = 12 MINUTES
TIME = 6 MINUTES
TIME = 22 MINUTES
TIME = 12 MINUTES
TIME = 6 MINUTES

FIGURE 10.—Chart showing relation between wind velocity, moisture content, time from start, and probable rate of perimeter increase, for surface fires in ponderosa pine needles on level ground.

V are zero. This value, so derived, is 6.35, a constant for any time. The final equation is:

$$p_t=6.35-k'\,M+k''\,V \qquad (2)$$

in which

p=rate of increase in perimeter in feet per minute
t=time in minutes from start of fire
k' and k''=constants determined from table 3
V=wind velocity in miles per hour
M=moisture content percent

THE EFFECT OF SLOPE

Inasmuch as forest topography is usually mountainous, and slope is recognized as an important factor in spread, this discussion would be incomplete without some consideration of the slope factor, which has been omitted up to this point mainly to simplify the problem. Studies of slope were conducted under both laboratory and field condi-

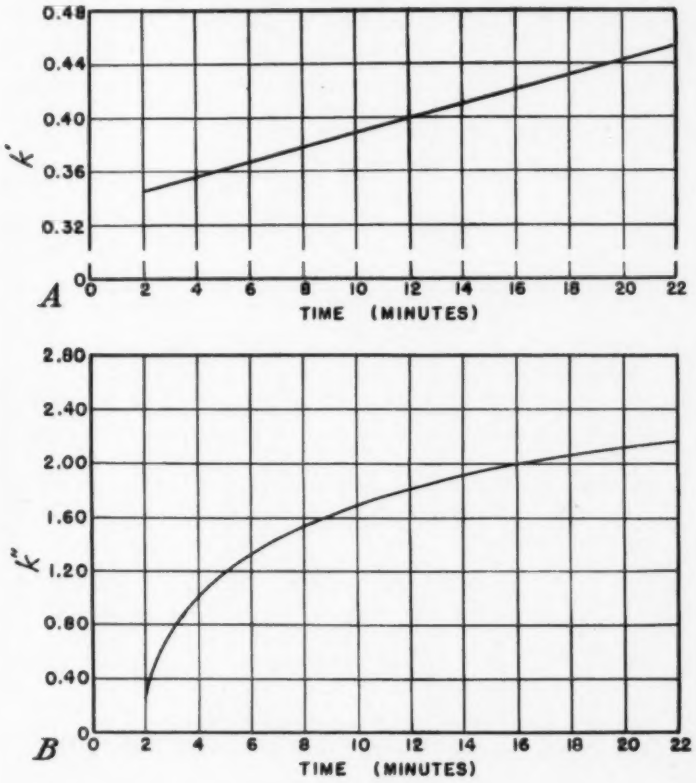

FIGURE 11.—*A*, effect of time on constant k' in equation $p=6.35-k' M+k'' V+f(SV)$. *B*, effect of time on constant k'' in equation $p=6.35-k' M+k'' V+f(SV)$.

tions. Field studies were in all respects similar to those described for fires on level ground.

In the study in the forest fire laboratory of the University of California a series of small fires were allowed to spread in a 4- by 10-foot burning pan at zero wind velocity and at slopes varying from 5 to 50 percent. Because of the small scale of the experiments, ponderosa pine needles were cut to a uniform length of 1½ inches to produce a slow-burning, uniform fuel. It was impractical in these studies to measure perimeter increase, linear spread being used instead. Previous studies had shown that linear spread was closely related to increase

in perimeter, and that generalizations true of one were applicable to the other.

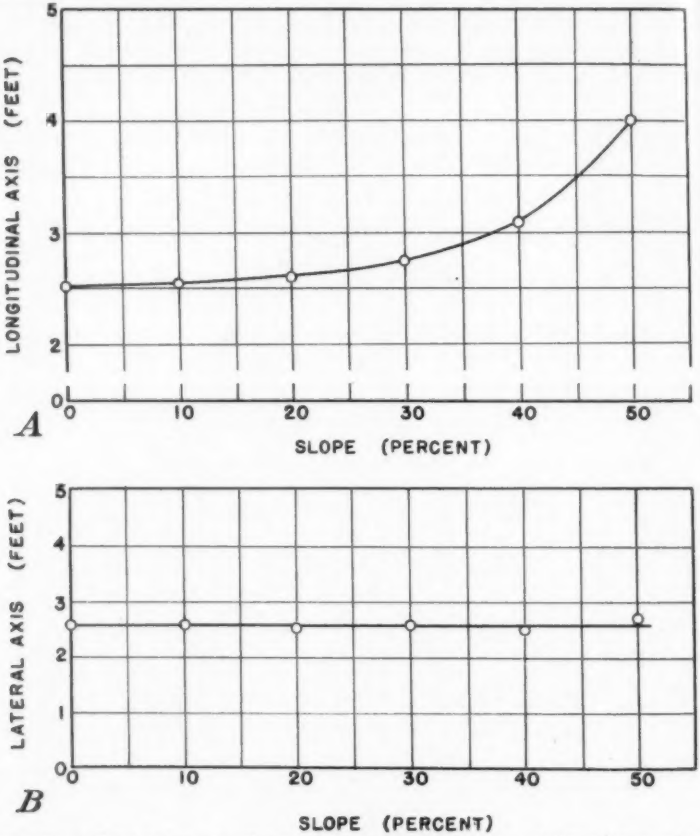

FIGURE 12.—*A*, Effect of slope on longitudinal axis of fires in feet at 3 minutes. *B*, Effect of slope on lateral axis of fires in feet at 3 minutes. Basis for *A* and *B*: 59 laboratory fires under constant moisture content and 0 wind velocity.

TABLE 3.—*Values of k', k'', K', and K'', for calculating rate of perimeter increase and total perimeter, equations 3 and 4*

Time (minutes)	k'	k''	K'	K''	Time (minutes)	k'	k''	K'	K''
2	0.35	0.26	0.69	0.52	13	0.41	1.85	4.85	16.44
3	.35	.74	1.04	1.26	14	.41	1.89	5.26	18.33
4	.36	1.00	1.40	2.26	15	.42	1.94	5.68	20.27
5	.36	1.20	1.76	3.46	16	.42	1.98	6.10	22.25
6	.37	1.33	2.13	4.79	17	.43	2.02	6.53	24.27
7	.37	1.44	2.50	6.23	18	.43	2.05	6.96	26.32
8	.38	1.53	2.88	7.76	19	.44	2.08	7.40	28.40
9	.38	1.61	3.26	9.37	20	.44	2.11	7.85	30.51
10	.39	1.68	3.65	11.05	21	.45	2.14	8.30	32.65
11	.40	1.74	4.05	12.79	22	.45	2.16	8.75	34.81
12	.40	1.80	4.45	14.59					

The important contributions of the laboratory study were (1) an indication of the type of curve representing the effect of slope on increase on the longitudinal axis and (2) evidence that slope had apparently no effect on the spread of fire at right angles to the slope direction; these indications are illustrated in figure 12. This study did not result, however, in any quantitative evaluation of the relative effect of slope, moisture, and wind upon rate of spread.

The field study comprised 46 fires at slopes of 10 to 30 percent. These were too few to permit the type of analysis used in determining

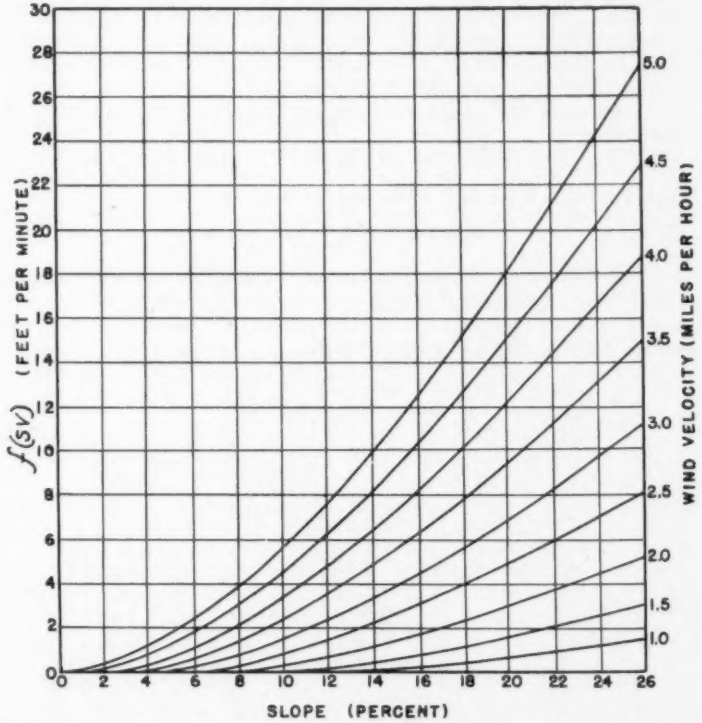

FIGURE 13.—Probable increase in rate of spread for slope fires over values for level ground for various slopes and wind velocities.

wind, moisture, and time relationships. It was decided, therefore, to determine the approximate relation of slope and perimeter through the use of the relationships already determined for fires on level ground, considering the deviations from the level ground perimeters as the influence of slope. When this was attempted, it was found that the size of the deviations depended largely upon the wind velocity at the period, or, in other words, that slope and wind were jointly correlated. Accordingly, the data were classified on the two variables, wind and slope, and deviations for each slope and wind-velocity class determined. The resulting relationships are shown in figure 13.

It seems apparent from a consideration of these curves that the influence of slope on rate of spread is inconsiderable at low wind velocities but that with higher wind, slope becomes increasingly important. The indicated increase due to slope may in many cases approach the original values on level ground. For instance, at moisture content of 5 percent, wind 4 miles per hour, and time 20 minutes, the rate of spread on level ground is 12.6 feet per minute. Under the same conditions but with a slope of 20 percent, the correction to be applied is 12.2 feet, resulting in a total indicated increase of 24.8 feet.

The slope measurements used in the analysis were the slope percent in the direction of the greatest spread, which corresponded closely to the prevailing wind direction. The relationships shown on slope are based on relatively scant data and are therefore not of comparable accuracy to the wind and moisture curves.

As a result of the analysis explained above, equation 2 may now be rewritten

$$p_t = 6.35 - k' M + k'' V + f(SV) \qquad (3)$$

Values of $f(SV)$ may be obtained from table 4.

ESTIMATING TOTAL PERIMETER

It is apparent that, for any values of wind and moisture within the range of data available, it is possible to calculate the total perimeter at any time interval up to 22 minutes from the relationships already explained and expressed in equation 3.

TABLE 4.—*Values of $f(SV)$ for calculating rate of perimeter increase and total perimeter, equations 3 and 4*

V=wind velocity per hour (miles)	S=slope in percent as indicated						V=wind velocity per hour (miles)	S=slope in percent as indicated					
	0	5	10	15	20	25		0	5	10	15	20	25
0	0	0	0	0	0.1	0.2	3.0	0	0.2	1.6	4.0	7.0	10.5
0.5	0	0	0	0	.2	.5	3.5	0	.4	2.5	5.6	9.5	13.9
1.0	0	0	0	.2	.6	1.2	4.0	0	.8	3.4	7.3	12.2	17.7
1.5	0	0	.2	.7	1.6	2.8	4.5	0	1.3	4.5	9.2	15.0	21.6
2.0	0	0	.4	1.6	3.0	4.8	5.0	0	1.8	5.6	11.2	18.0	25.8
2.5	0	0	.9	2.6	4.8	7.5							

An equation to express total perimeter with constant wind and moisture conditions directly may be derived from equation 3, as follows:

$$P_t = 6.35t - (K_t')M + (K_t'')V + f(SV)t$$

in which

P_t = total perimeter at a particular time
t = time in minutes from start of fire
V = wind velocity in miles per hour
K_t' = factor to be multiplied by moisture content (table 3)
M = moisture content in percent
K_t'' = factor to be multiplied by wind (table 3)
$f(SV)$ = factor to be multiplied by time for slope fires (table 4)

The derivation of the above expression is as follows:

From equation 3, the perimeter at end of 2 minutes would be

$$p_2=2(6.35)-2k_2'M+2k_2''V+2f(SV)$$

and the perimeter increase in the third minute would be

$$p_3=6.35-k_3'M+k_3''V+f(SV)$$

for the fourth minute

$$p_4=6.35-k_4'M+k_4''V+f(SV)$$

and for the nth minute

$$p_t=6.35-k_t'M+k_t''V+f(SV)$$

Total perimeter at end of any time would be

$$P_t=p_2+p_3+p_4+\text{----}+p_t$$

Adding the above equations and factoring

$$P_t=6.35t-(2k_2'+k_3'+k_4'+\text{----}+k_t)M+(2k_2''+k_3''+k_4''+\text{----}+k_t'')V+f(SV)t$$

Let $K_t'=(2k_2'+k_3'+k_4'+\text{----}+k_t')$ and $K_t''=(2k_2''+k_3''+k_4''+\text{----}+k_t'')$

Then, as already expressed,

$$P_t=6.35t-(K_t')M+(K_t'')V+f(SV)t \qquad (4)$$

Values of K_t' and K_t'' have also been arranged in table 3.

Values of $f(SV)$ have been arranged in table 4 for ease in computation.

To illustrate the manner in which total perimeter increases with time, figures 14 to 17 have been prepared. These figures illustrate the characteristic behavior noted by Show (*6*).

ACCURACY OF ESTIMATE

To determine the error of estimate of the derived predictions from the derived relationships, 350 cases of rate of spread for a 2-minute period were drawn at random from the 1,153 cards for fires on level ground and estimates from the appropriate equation compared to the observed values. The results follow.

Fires on level:		
Average perimeter increases	feet	11. 4
Standard deviation of average perimeter increase	do	6. 2
Standard error of estimate	do	4. 3
Index of alienation		0. 69
Index of correlation		0. 72

As there were in all only 372 2-minute cases of fires on slopes, the entire sample was used in the computation of the measures listed below:

Fires on slopes:		
Average perimeter increases	feet	22. 9
Standard deviation of average	do	16. 5
Standard error of estimate	do	12. 7
Alienation index		0. 77
Correlation index		0. 64

The absence of higher correlation is due in part to inadequacy of measurement of perimeter, moisture, and wind, as well as to failure to include all the factors affecting the spread of fire. On a fast-burning fire it is impossible to approximate the location of the line closer than 1 foot, and this error is magnified in terms of perimeter. Measurements of moisture are only average values for the entire plot

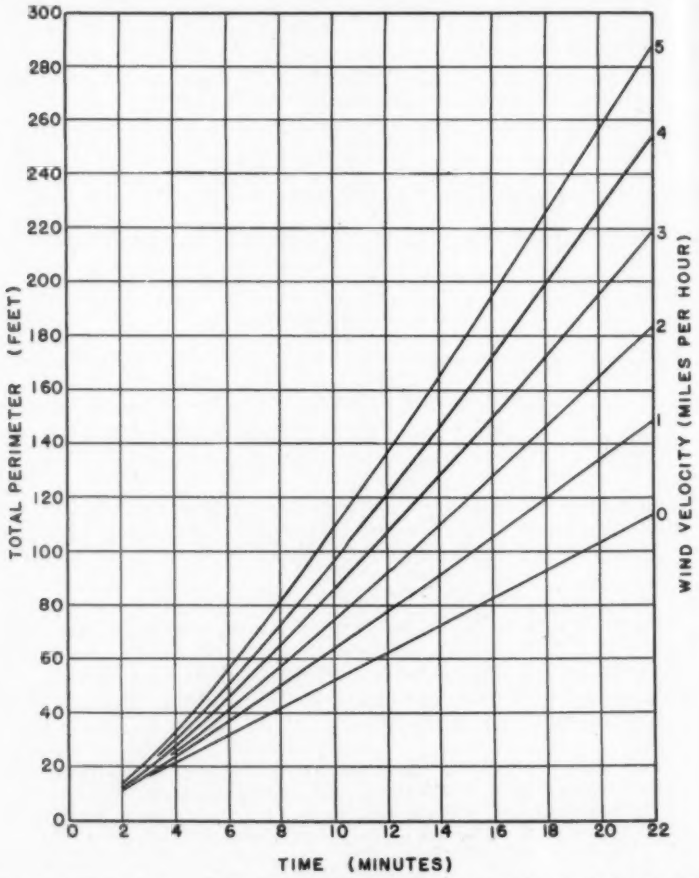

FIGURE 14.—Probable total perimeter of fires burning under various constant wind velocities at moisture content 3 percent.

and cannot be expected to approximate closely the moisture content of the particular portion of the litter in which the fire is spreading at a given time interval. Measurements of wind velocity, although taken by 2-minute time intervals, may also fail to show accurately the wind movement near the head of the fire. These errors are not cumulative but compensating, and greater correlation may accordingly be expected when the relationships are used in the estimation of total per-

imeter. That improved errors of estimate result when total perimeter is used instead of perimeter increase, is shown by table 5, in which indexes of correlation and errors of estimate have been derived for each 2-minute period from a comparison of the estimated and actual total perimeters. Table 5 also gives comparisons of actual and estimated perimeters on slope.

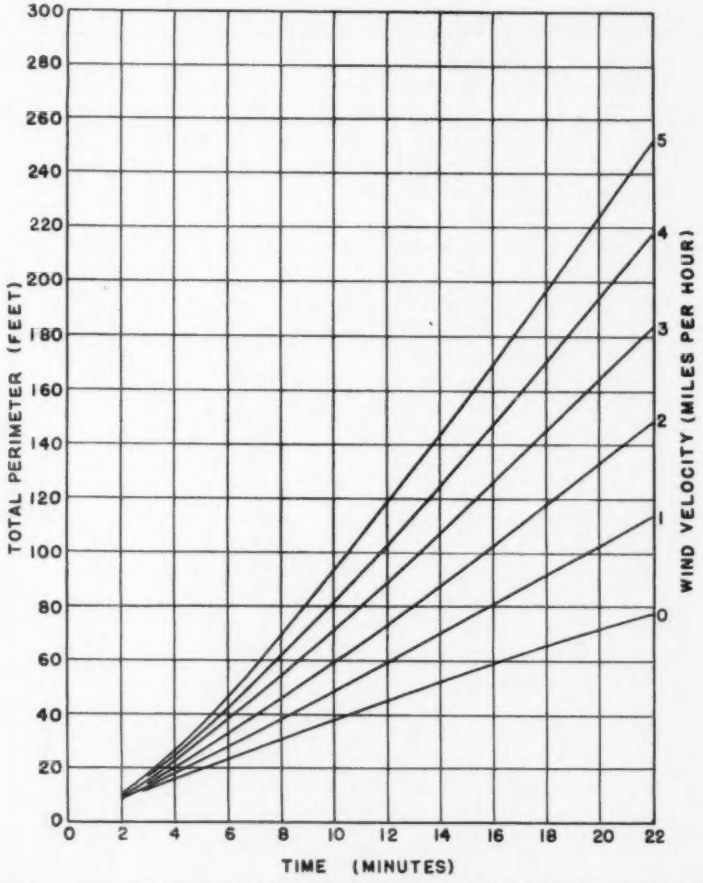

FIGURE 15.—Probable total perimeter of fires burning under various constant wind velocities at moisture content 7 percent.

The measurements indicate that, although it is not possible to estimate rate of perimeter increase with a high degree of accuracy, yet, when the relationships derived are applied to estimates of total perimeter, a smaller error in proportion to the observed or dependent value results. This fact has considerable bearing on the practical side of the problem.

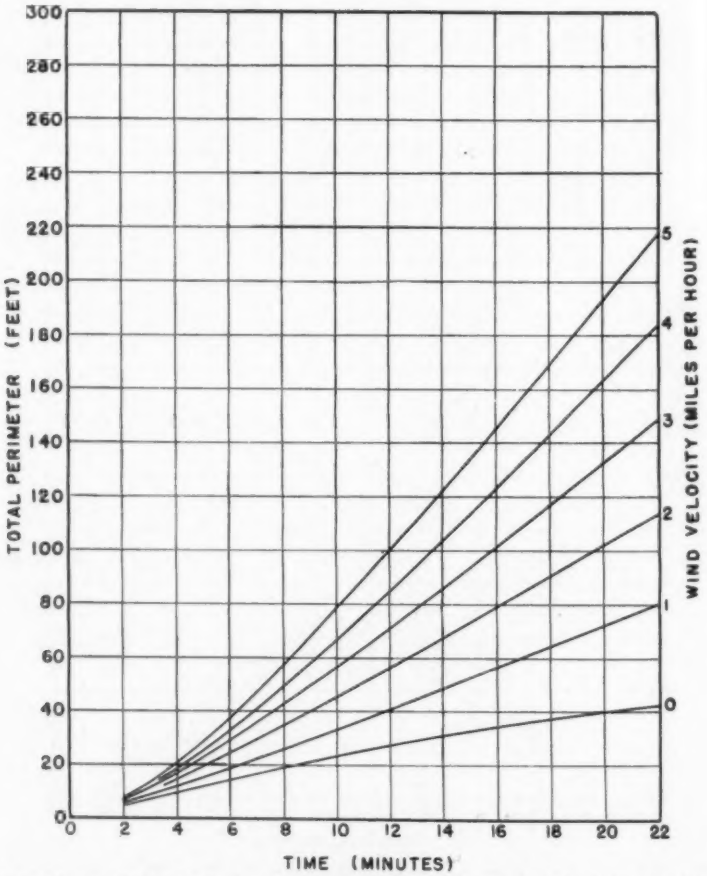

FIGURE 16.—Probable total perimeter of fires burning under various constant wind velocities at moisture content 11 percent.

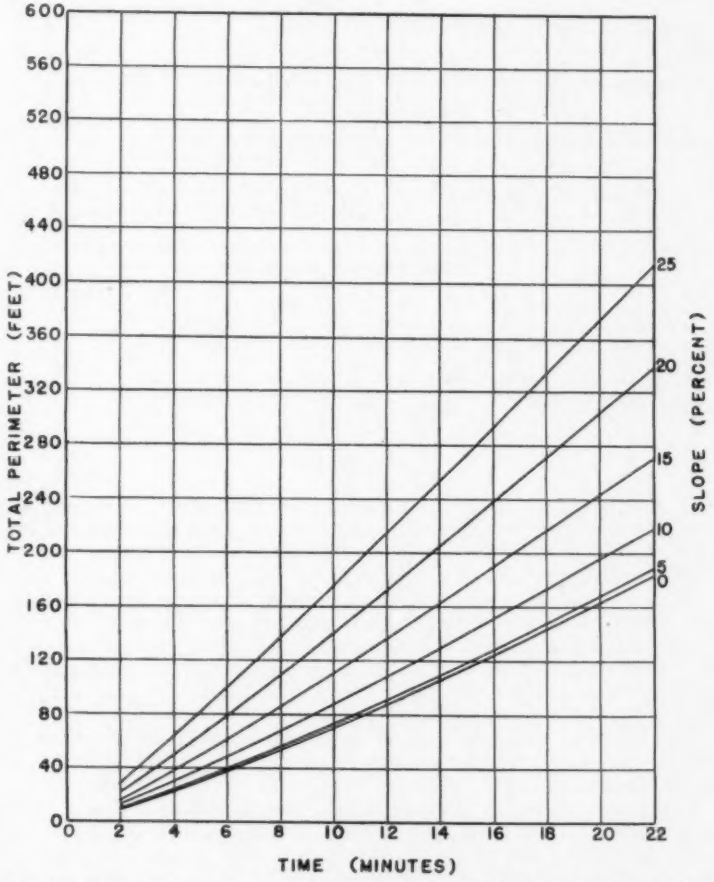

FIGURE 17.—Probable total perimeter of fires on various slopes for moisture content 7 percent and wind velocity 3 miles per hour.

TABLE 5.—*Summary of results in the application of the derived relationships to the computation of total perimeter of test fires on level and sloping ground at each 2-minute time interval from start of fire*

FIRES ON LEVEL GROUND

Time (minutes)	Cases	Average perimeter		Standard deviation of average actual perimeter	Standard error of estimate		Aliena-tion index	Correla-tion index
		Actual	Calculated					
	Number	*Feet*	*Feet*	*Feet*	*Feet*	*Percent*		
2	118	7.5	7.6	2.6	2.1	28.0	0.81	0.59
4	118	17.7	17.7	6.4	4.5	25.4	.70	.71
6	118	28.9	28.6	9.8	6.2	21.5	.63	.78
8	118	40.0	40.0	15.0	9.4	23.5	.63	.78
10	118	51.2	51.6	18.6	11.1	21.7	.60	.80
12	117	63.5	63.0	22.6	13.7	21.6	.61	.79
14	114	75.4	74.7	27.1	16.0	21.2	.59	.81
16	109	87.0	86.1	31.5	16.5	19.0	.52	.85
18	96	97.7	96.5	38.9	19.2	19.7	.49	.87
20	71	102.3	102.8	40.9	17.2	16.8	.42	.91
22	56	112.6	112.6	51.2	19.7	17.5	.38	.92

FIRES ON SLOPING GROUND

2	46	12.1	15.5	7.2	6.8	56.2	0.94	0.34
4	46	32.4	34.9	18.5	10.2	31.5	.55	.84
6	46	58.5	57.4	33.2	18.4	31.5	.55	.84
8	46	87.2	82.8	52.1	30.4	34.9	.58	.81
10	42	105.5	102.4	64.5	38.5	36.5	.60	.80
12	36	116.2	122.2	50.6	35.5	30.6	.71	.70
14	31	128.1	139.8	52.5	37.8	29.5	.72	.69
16	27	144.3	166.3	59.5	41.6	28.8	.70	.71

SUMMARY

In this study of rate of spread of small surface fires in selected even-aged second-growth stands of *Pinus ponderosa*, records were analyzed of about 160 fires with burning periods of 16 to 22 minutes.

The influence of both moisture and wind is described as linear, with the slope of the curves varying with the time factor. Where fires burned with low wind, the maximum rate of spread as controlled by the moisture content was soon attained. With higher velocities, the period required to attain maximum rate of spread increased, and in some cases did not yet reach that maximum at the end of the 22-minute period, the time limit of the test fires.

The effect of slope on rate of spread was found to be curvilinear and largely dependent for its influence upon the occurrence of winds in the direction of the slope.

Empirical formulas derived from the smoothed curves permit estimates of rate of perimeter increase or total perimeter at any time interval within the limits of the data. The generalizations made appear highly significant, and prediction of total perimeter may be possible within a reasonable error of estimate.

Extension of rate-of-spread studies to other types is dependent to a large extent upon research leading to methods of evaluation of the factor of fuel variation. With progress in present studies of fuels, similar studies in more complex forest types are contemplated.

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ANATOMY OF THE LEAF AND STEM OF GOSSYPIUM[1]

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INTRODUCTION

Because of the great commercial importance of cotton fibers, their structure at various stages of development has been carefully studied. An indication of the work that has been done along this line may be gained from the papers of Dischendorfer (*6*),[3] Youngman and Pande (*53*), and Kerr (*21*), which give a number of literature citations. Structure of the seed (*14, v. 3; 32; 33; 34; 35; 36; 37*) and that of the boll (*14, v. 3; 40*) are intimately connected with fiber production and have received considerable attention. The anatomy of the cotton flower has also been investigated to some extent (*7; 10; 14, v. 3–4*).

The structure of the vegetative organs of *Gossypium*, although closely connected with the various plant functions and hence influencing fiber yield, has received comparatively little attention. Some anatomical characteristics of seedlings of *G. hirsutum* × *G. barbadense* were depicted by Heim de Balsac (*14, v. 1*). The relation of the various reproductive and vegetative parts of mature cotton plants of different types has been repeatedly described (*4, 5, 16, 38*), and an attempt has been made by Zaitzev (*54*) to ascertain the gross morphological characteristics of Old World cottons with a haploid chromosome number of 13 and New World cottons with a haploid chromosome number of 26, but descriptions of the histology of the vegetative organs are wholly inadequate. A brief account of the anatomy of the various vegetative organs of an unnamed species of *Gossypium* was given by Flatters (*9*), rather detailed reports of the microscopic structure of the roots (*11*) and the transition region (*44*) of *G. hirsutum* L. have been made, the ontogeny of the main stem and fruiting branches has been traced (*10*), and some histological characteristics of leaves and stems of *G. herbaceum* L., *G. barbadense* L. (*14, v. 3*), and *G. hirsutum* × *barbadense* (*14, v. 2*) have been figured; but there is no consecutive account of the anatomical characteristics of the vegetative organs of the main groups of species or of the genus as a whole. Since there is considerable disagreement concerning the taxonomy of the genus and since microscopic and endomorphic characters when considered in conjunction with macroscopic exomorphic ones are often helpful in solving taxonomic problems, the present anatomical study of the genus *Gossypium* was undertaken.

MATERIAL AND METHODS

Although this investigation was limited to nonfruiting branches, special attention was paid to anatomical characteristics that might be useful in distinguishing between American wild cottons with 13 haploid chromosomes (*12, 19, 20*) which have been excluded from the genus

[1] Received for publication October 13, 1937; issued August 1938.

[2] The material examined was made available for study through the courtesy of T. H. Kearney and J. M. Webber, of this Division.

[3] Italic numbers in parentheses refer to Literature Cited, p. 283.

ANATOMY OF THE LEAF AND STEM OF GOSSYPIUM [1]

By IRMA E. WEBBER [2]

Collaborator, Division of Cotton and Other Fiber Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

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Gossypium by some taxonomists, Old World cottons with 13 haploid chromosomes, and New World cottons with 26 haploid chromosomes. For comparative purposes a limited number of *Gossypium* hybrids and representatives of other genera of the Hibisceae were also included in the study. The species examined and the groups to which they belong are:

Old World cottons with 13 haploid chromosomes: *Gossypium africanum* Watt, *G. anomalum* Wawra and Peyr., *G. arboreum* L., *G. cernuum* Tod., *G. herbaceum* L., *G. intermedium* Tod., *G. nanking* Meyen, *G. neglectum* Tod., *G. sanguineum* Hasskl., *G. stocksii* Mast., *G. sturtii* F. Muell., *G. transvaalense* Watt.

American wild cottons with 13 haploid chromosomes: *Gossypium armourianum* Kearney, *G. davidsonii* Kellogg, *G. harknessii* Brandeg., *G. klotzschianum* Anderss., *G. thurberi* Tod. (*Thurberia thespesioides* A. Gray).

New World cottons with 26 haploid chromosomes: *Gossypium barbadense* L., *G. brasiliense* Macf., *G. contextum* Cook and Hubbard, *G. darwinii* Watt, *G. hirsutum* L., *G. hopi* Lewton, *G. peruvianum* Cav., *G. purpurascens* Poir., *G. schottii* Watt, *G. tomentosum* Nutt.

Doubtful species of *Gossypium* and members of related genera: *Gossypium kirkii* Mast., *Alyogyne hakeaefolia* (Giord.) Alef., *Erioxylum aridum* Rose and Standl., *Hibiscus brackenridgei* A. Gray, *H. tiliaceus* L., *Kokia drynarioides* (Seem.) Lewton, *K. rockii* Lewton, *Lagunaria patersonii* G. Don, *Thespesia lampas* (Cav.) Dalz., *T. populnea* Soland., and *Shantzia garckeana* Lewton.

All of the material examined was taken from plants grown in the field at the Rubidoux Laboratory,[4] Riverside, Calif. Much of the material was sectioned when fresh, but some of it was first killed and fixed in formalin-acetic alcohol and embedded in paraffin. Safranine was used to stain some sections; the remainder were left unstained.

LEAF ANATOMY

EPIDERMIS

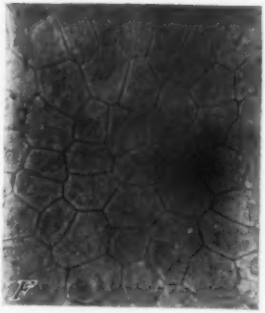
The ordinary epidermal cells over chlorenchyma may be straight-walled or very sinuate in surface view. In most species their lateral walls are much less sinuous in the upper epidermis than in the lower epidermis, where stomata are more numerous (pl. 1, *A*, *B*). However, in some species the lateral walls of epidermal cells are characteristically rather straight on both upper and lower leaf surfaces (*C*, *D*). On vertically transcurrent veins the epidermal cells are longer and narrower than elsewhere on the lamina, the long axis of the cell being parallel to the course of the vein (*E*). Over lysigenous cavities in the mesophyll, the epidermal cells are concentrically arranged and generally smaller than the surrounding cells (*F*).

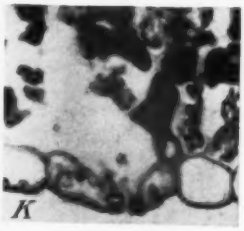
According to Flatters (*9*, *p. 43*) "The epidermis of the upper [leaf] surface consists of closely-packed cells with resin-cells distributed among them * * *." What he here designates as "resin-cells" is not clear to the writer. In his figure of a cross section of a stem the lysigenous cavities are so labeled, but their absence in the epidermis

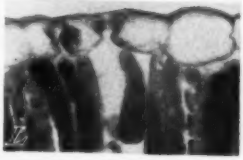
[4] Maintained cooperatively by the U. S. Department of Agriculture and the California Agricultural Experiment Station.

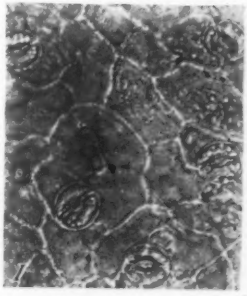
EXPLANATORY LEGEND FOR PLATE 1.

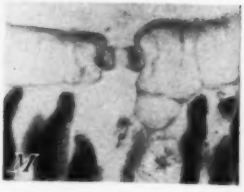
Epidermis of *Gossypium* leaves. × 312. *A–J*, Surface views showing comparative shape and size of ordinary epidermal cells and stomata. *A* and *B*, *G. brasiliense*: *A*, From upper side of leaf; *B*, from lower side of leaf. *C* and *D*, *G. harknessii*: *C*, From upper side of leaf; *D*, from lower side of leaf. *E* and *F*, *G. peruvianum*: *E*, Epidermis of a vein; *F*, epidermis over a lysigenous cavity in the mesophyll. *G–J*, Epidermis from lower surfaces of leaves: *G*, *G. hirsutum* var. Acala; *H*, *G. hirsutum* × *G. cernuum*; *I*, *G. armourianum*; *J*, *G. hirsutum* × *G. armourianum*. *K–M*, Leaf sections showing position of stomata: *K*, *G. contextum*, lower epidermis; *L*, *G. arboreum*, upper epidermis; *M*, *G. harknessii*, upper epidermis.











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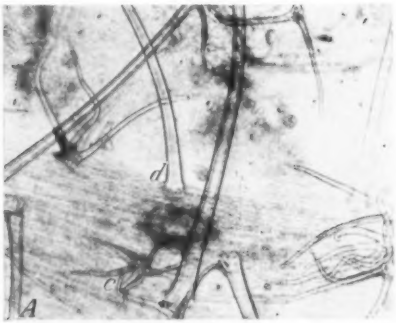

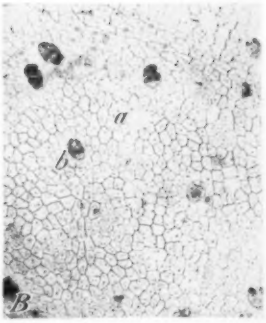

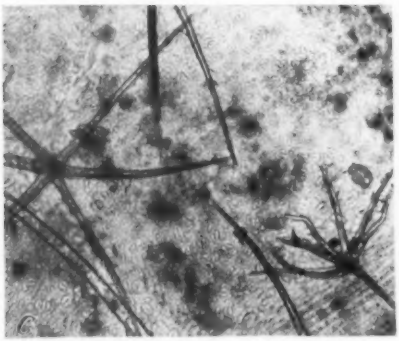

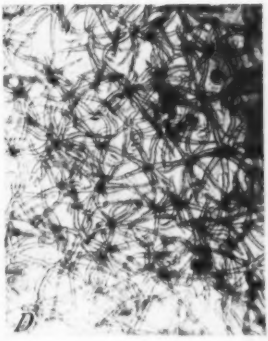

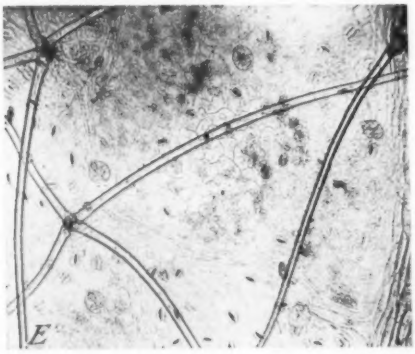

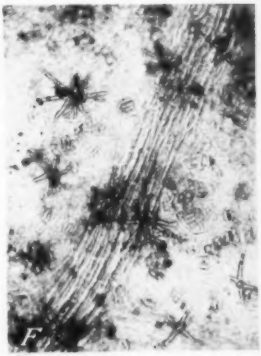

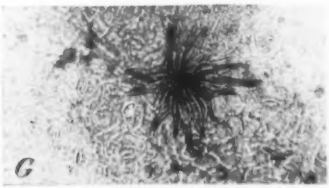

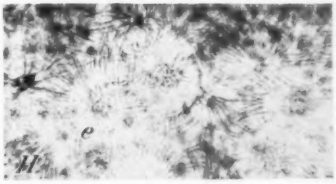

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of leaves suggests that he either did not distinguish clearly between epidermal and subepidermal tissue, or applied the term "resin-cells" to some other structure as well as to the lysigenous cavities. In the latter case, ordinary epidermal cells with colored contents, mucilage cells, or minute, depressed capitate hairs may be meant.

Ordinary epidermal cells with colored, usually purplish or reddish, cell sap are of scattered occurrence in most species of *Gossypium*. In green-leaved plants they commonly adjoin the guard cells of stomata and are not nearly so numerous as the hyaline epidermal cells. In reddish-leaved plants, such as *G. purpurascens* and the Red Acala variety of *G. hirsutum*, they are not restricted to the vicinity of stomata and may be more numerous than hyaline epidermal cells. The inheritance of red plant color in cotton plants has been discussed by Ware (*49*).

Although mucilage cells were reported by Dumont (*8*) as completely wanting in *Gossypium* and as very rare throughout the Hibisceae, according to Kuntze (*22*) they are characteristic of both the upper and the lower epidermis of the leaves of all Hibisceae. They are apparently lacking or inconspicuous in the epidermis of *Kokia*, *Shantzia*, *Erioxylum*, and most species of *Gossypium*, but fairly numerous in that of *G. kirkii* (pls. 2, *B*, *a*; 3, *M*, *a*), *G. klotzschianum* (pl. 3, *B*, *a*), *Thespesia*, *Hibiscus*, and *Lagunaria*. As a rule, they are considerably larger than the adjoining cells, and more common in the upper than in the lower epidermis. The distribution and structure of mucilage cells in a number of malvaceous genera, chiefly representative of tribes other than the Hibisceae, have been discussed by Trécul (*46*), Walliczek (*48*), and Nestler (*28*).

Heim de Balsac (*14*, *v. 3*) depicted stomata in the lower but not the upper epidermis of the leaves of *Gossypium herbaceum* and *G. barbadense*, while stomata were reported by Flatters (*9*) as few or absent in the upper epidermis of the leaves of *Gossypium* and by Kuntze (*22*) as lacking in the upper epidermis of *G. drynarioides* Seem. The latter species is now referred to the genus *Kokia* and was found by the writer to have a few widely scattered stomata on the upper leaf surface. In all species of *Gossypium* examined, stomata are present on both upper and lower leaf surfaces but are more numerous on the lower surface. In some species the difference between the average number of stomata per square millimeter of the upper and the lower epidermis of a leaf is very marked, while in others it is comparatively slight. For example, when stomatal counts were made near the centers of mature leaf blades in areas free from large veins, the average number of stomata per square millimeter of upper and lower leaf surfaces were, respectively, 122 and 159 in *G. harknessii*, and 40 and 218 in *G. peruvianum*. The correlation indicated by Kuntze for most Malvaceae between a dense coating of hairs and the presence of stomata in the upper epidermis, or dense hairy covering and relatively high stomatal number in the lower epidermis, does not hold true in *Gossypium*. In leaves of the species examined by the writer the average number of stomata per square millimeter of the upper epidermis ranged

EXPLANATORY LEGEND FOR PLATE 2.

Leaf epidermis of *Gossypium* and related genera showing various types of hairs. × 80. *A*, *G. intermedium*; *B*, *G. kirkii*; *C*, *G. sanguineum*; *D*, *G. tomentosum*; *E*, *G. peruvianum*; *F*, *G. thurberi*; *G*, *Thespesia populnea*; *H*, *Lagunaria patersonii*. *a*, Mucilage cell; *b*, capitate hair; *c*, stellate hair; *d*, simple hair; *e*, peltate scale.

from 40 in *G. peruvianum* to 170 in *G. intermedium*, while average stomatal numbers per square millimeter of the lower epidermis varied from 80 in *G. tomentosum* to 280 in *G. anomalum*.

Within the genus *Gossypium* the stomatal apparatus of leaves varies from roundish (pl. 1, *H*, *I*) to elliptic (*A*, *B*, *C*, *D*, *E*, *G*, *J*) in surface view, the latter form dominating. Twin and malformed stomata are occasionally present, being somewhat more numerous in certain hybrids than in their parents. The normal stomatal apparatus of mature leaves varies in average length from about 24μ to 32μ and in average width from about 16μ to 24μ. Within a species there are no appreciable differences in size or shape between stomata of the upper leaf surface and those of the lower leaf surface, some variation generally occurring on both surfaces. Because of the similarity of stomata in most of the species, stomatal size in interspecies hybrids of *Gossypium* is generally of little significance. At times, however, when a species with relatively large stomata (*G*) and one with small stomata (*I*) are crossed, stomatal size of the hybrid is clearly intermediate between that of the parents (*J*). Some such hybrids show a wider range in stomatal size than most of the species (*H*). Stomata may be level with the ordinary epidermal cells (*L*), slightly above the general epidermal surface (*K*), or slightly below it (*M*), those on a single leaf often being in more than one position.

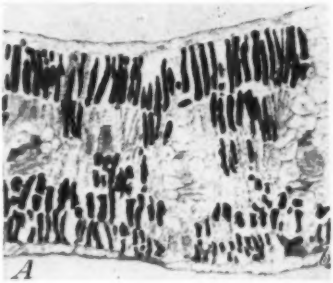
Exclusive of epidermal outgrowths, the thickness of the epidermis on mature leaves of *Gossypium* varies considerably. In some species and hybrids, notably *G. armourianum* (pl. 3, *A*), *G harknessii*, *G. thurberi* (*C*), G. *armourianum* × *G. harknessii*, *G. thurberi* × *G. sturtii*, *G. sturtii* × *G. harknessii*, and *G. hirsutum* × *G. sturtii*, the upper and lower epidermis of a leaf are of approximately the same thickness. In such plants the average thickness of the leaf epidermis over chlorenchyma varies from about 16μ to 32μ. In the majority of species the upper epidermis of a leaf is thicker than the lower epidermis. The difference in thickness may be relatively slight as in *G. barbadense*, *G. peruvianum* (*E*), and *G. anomalum* (*I*), or considerable as in *G. klotzschianum* (*B*), *G. hirsutum* (*F*), and *G. herbaceum* (*J*). In leaves with upper and lower epidermis of different thicknesses, the upper epidermis varies in average thickness from about 14μ to 32μ, and the thickness of the lower epidermis ranges from about 10μ to 32μ. Over large veins the epidermal cells often have thicker outer walls than elsewhere on the lamina.

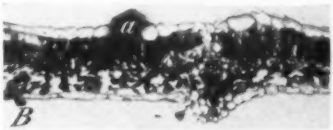
Three types of epidermal outgrowths occur on the leaves and stems of *Gossypium*. The ontogeny of each hair type has been traced by Youngman and Pande (*53*) and shows a marked similarity to that of comparable trichomes described by Rauter (*30*) in *Malva*.

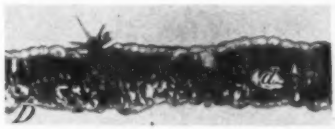
Multicellular capitate hairs, sometimes called glandular hairs (*43*), club-shaped bodies (*53*), or septate papillae (*45*), were observed on both the upper and the lower leaf surfaces of all species of *Gossypium* examined. They are more numerous than other types of trichomes on the mature leaves of *G. armourianum*, *G. harknessii*, *G. barbadense*, *G. brasiliense*, *G. contextum*, *G. darwinii*, *G. hirsutum*, *G. hopi*, *G.*

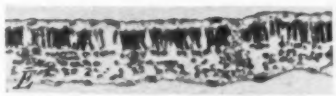
EXPLANATORY LEGEND FOR PLATE 3.

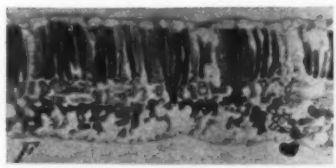
Cross sections of leaf blades showing structure of the epidermis and mesophyll. ×80. *A*, *Gossypium armourianum*; *B*, *G. klotzschianum*; *C*, *G. thurberi*; *D*, *Erioxylum aridum*; *E*, *G. peruvianum*; *F*, *G. hirsutum*; *G*, *G. tomentosum*; *H*, *G. barbadense*; *I*, *G. anomalum*; *J*, *G. herbaceum*; *K*, *G. cernuum*; *L*, *G. sturtii*; *M*, *G. kirkii*. *a*, Mucilage cell; *b*, capitate hair; *c*, stellate hair; *d*, lysigenous cavity in mesophyll.

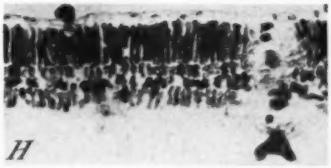


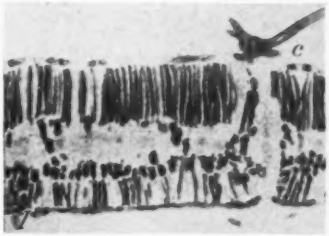


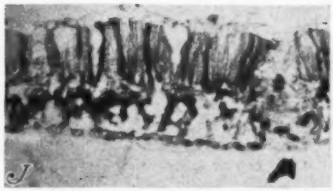


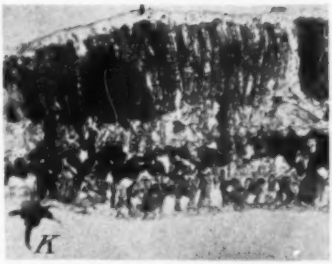


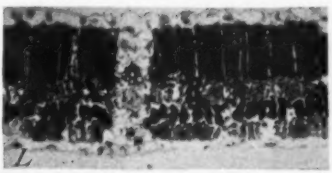


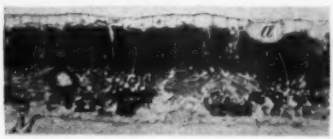












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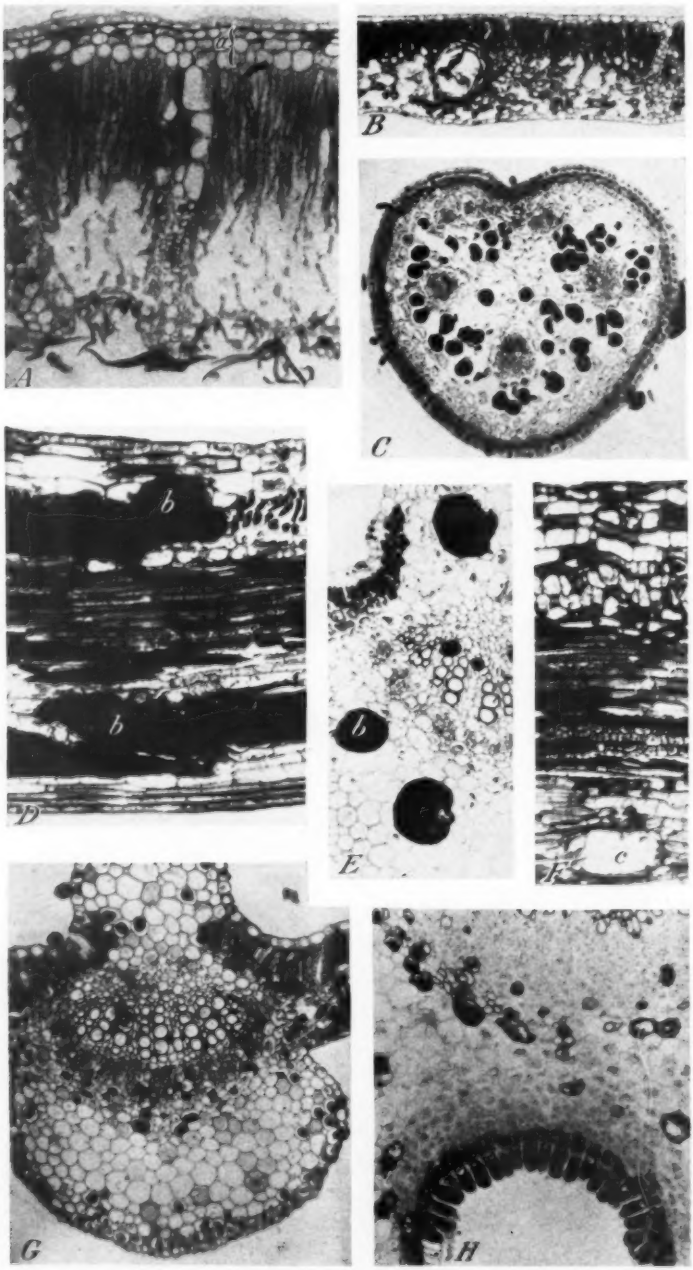

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peruvianum, *G. purpurascens*, *G. schottii*, and *G. kirkii* (pl. 2, *B*), but are comparatively rare even in young leaves of *G. sturtii*. They vary considerably in size, shape, color of contents, and the extent to which their bases are depressed below the level of non-trichome-bearing cells (pl. 3, *A*, *B*, *F*, *H*, *I*). They are not confined to the genus *Gossypium*, having been observed also in the genera *Alyogyne* (pl. 4, *C*), *Lagunaria*, *Hibiscus*, *Kokia*, *Thespesia*, and *Shantzia*. Other types of capitate and glandular hairs characteristic of various malvaceous genera have been figured by Janda (*18*).

Stellate hairs, characteristic of the family Malvaceae, were present on the leaves of all species of *Gossypium* examined. Their absence in some species of this genus has been pointed out by Hubbard (*16*), who reported a South American species with simple hairs, and by Youngman and Pande (*53*), who mentioned mutant forms of both Old World and New World cottons without stellate hairs or their derivatives. The stellate hairs of *Gossypium* leaves are commonly more abundant on the lower than on the upper surface, and frequently more abundant along the major veins than elsewhere on the lamina. They are often more conspicuous on the petiole than on the leaf blade. Some indication of their diversity in size, form, and distribution on lower leaf surfaces of various species of *Gossypium* and related genera is given in plates 2, *A*, *C*, *D*, *E*, *F*; 3, *C*, *D*, *G*, *H*, *I*, *J*, *K*; and 4 *A*, *C*.

Simple hairs, apparently derivatives of stellate hairs, are generally scattered among the stellate hairs on the mature leaves of most species of *Gossypium*. Usually they resemble a single ray of a stellate hair in both form and size. However, in some species, for example, *G. africanum*, *G. arboreum*, *G. nanking*, and *G. neglectum*, they are both broader and longer than the individual rays of the stellate hairs with which they are associated (pl. 2, *A*). In species with stellate hairs of two distinct sizes, e. g., *G. sanguineum* (*C*), some of the simple hairs resemble the rays of the large stellate hairs and some resemble those of the small stellate hairs.

No peltate scales, sucn as are characteristic of the lower surfaces of the leaves of the related species *Thespesia populnea* (pl. 2, *G*) and *Lagunaria patersonii* (*H*), were observed in *Gossypium*. The distribution and characteristics of peltate scales in a number of families have been discussed by Bachmann (*2*).

HYPODERMIS

Of the species listed by Solereder (*43*) under the Malvaceae as having a many-layered epidermis or hypodermis, all but *Gossypium drynarioides* are members of the Bombacaceae. This species, now referred to the genus *Kokia*, resembles *Kokia rockii* in that it does not develop a hypodermis under Riverside conditions (pl. 4, *B*). Although scattered epidermal cells divided by horizontal walls are sometimes present in *Gossypium* and related genera, true hypodermis is apparently lacking in *Gossypium*. However, a well-developed hypodermis occurs in *Lagunaria patersonii* (*A*), which Dumont (*8*) reported,

EXPLANATORY LEGEND FOR PLATE 4.

Leaf sections of *Gossypium* and related genera. × 80. *A–C*, Cross sections showing characteristics of epidermis and mesophyll: *A*, *Lagunaria patersonii*; *B*, *Kokia drynarioides*; *C*, *Alyogyne hakeaefolia*. *D*, *Hibiscus tiliaceus*, longitudinal section of midrib. *E*, *H. brackenridgei*, cross section of midrib. *F*, *G. sanguineum*, longitudinal section of midrib. *G* and *H*, *G. schottii*, cross sections of midribs: *G*, Taken at about midpoint of vein; *H*, taken through nectary. *a*, Hypodermis; *b*, mucilage canal; *c*, lysigenous cavity.

under the name *Lagunea syuamea*, as having much elongated epidermal cells often divided transversely.

MESOPHYLL

The predominance of bifacial leaf structure in the Malvaceae has been pointed out by Solereder (*43*). Aside from the bombacaceous species he includes, he reports centric leaf structure only in *Malva parviflora*. In describing the anatomy of cotton leaves, Flatters (*9, p. 43*) states that the upper part of the mesophyll is composed of two layers of palisade cells. "The lower half of the mesophyll is made up of loosely arranged irregular cells with large air spaces between them * * *." The inapplicability of Flatters' description to the mesophyll of all species of *Gossypium* and the commoner occurrence of centric leaf structure than was indicated by Solereder (*43*) are evident from the account of structural differences in mesophyll within the genus *Gossypium* given by Magitt and Magitt (*25*). They stated that palisade parenchyma underlies the epidermis of only the upper surface of the leaf in American cottons and in hybrids between American and Asiatic cottons, but occurs beneath the epidermis on both upper and lower leaf surfaces in Asiatic cottons. This distinction between Old World and New World cottons does not apply to plants grown in the field at Riverside. Specimens examined by the writer showed that leaves of some species of the Old World group (pl. 3, *I, K, L*), of the American group with 26 pairs of chromosomes (*G, H*), and of the wild American group with 13 pairs of chromosomes (*A*) develop palisade underlying the epidermis of both the upper and the lower surface. Within each of these three groups of *Gossypium*, the leaves of some species are characterized by mesophyll composed of palisade tissue underlying the upper epidermis and spongy parenchyma underlying the lower epidermis (*B, C, E, F, J*). A less common type of centric leaf structure than that occurring in *Gossypium* was observed in the cotton relative *Alyogyne hakeaefolia* (pl. 4, *C*).

In structure as well as in distribution, the palisade tissue of *Gossypium* leaves shows greater diversity than was indicated by Flatters (*9*). In the leaves of *G. armourianum* (pl. 3, *A*) and *G. harknessii* there are areas in which palisade tissue extends from the upper to the lower epidermis and is commonly four or five cells thick. The palisade layers are more commonly one cell than two cells thick in leaves with palisade tissue restricted to the upper side or with clearly distinct upper and lower palisade layers. Palisade cells of plants grown in the field vary in length from about 30μ to 220μ and are commonly longer in the upper layer of palisade parenchyma than in the lower layer, when the latter is present.

The spongy parenchyma of *Gossypium* leaves is often more compact than Flatters (*9*) indicated. At times the form and arrangement of spongy parenchyma cells so closely approximates that of weak palisade tissue that a distinction between the two types of tissue is purely arbitrary.

Oblate or spherical cavities, usually 50μ to 170μ in diameter and commonly with dark-purplish or brownish contents (pl. 3, *C, M*), occur in the mesophyll of all species of *Gossypium* examined and in the mesophyll of *Erioxylum aridum* (*D*), *Kokia drynarioides* (pl. 4, *B*), *K. rockii*, *Thespesia lampas*, *T. populnea*, and *Shantzia garckeana*.

They were reported by Dumont (*8*) to be of schizogenous origin, but according to the earlier report of Von Höhnel (*15*) on similar cavities in the cotyledons of *Gossypium herbaceum* and the more recent work of Stanford and Viehoever (*45*) on various organs of *G. hirsutum*, they are formed lysigenously. Similar cavities have been referred to under a variety of names, including mucilage glands (*14, v. 2*), mucilage pockets (*8, 22*), resin cells (*9*), resin glands (*36*), black oil glands (*23*), internal glands (*45*), gossypol cavities (*52*), and mucilage canals (*18*). According to Stanford and Viehoever (*45*), the nature of the contents of the flattened cells surrounding the cavities is dependent upon whether they are developed in darkness or exposed to light.

VEINS

The veins of *Gossypium* leaves are mostly vertically transcurrent (pl. 3, *I, L*), but some of the smaller ones are embedded (*G*). The midribs and other large veins commonly project beyond the general level of the lamina on both upper and lower surfaces of the leaf (*A–I*). The relative thickness of the major veins and of the photosynthetic areas of leaves, as well as size and shape of major veins at comparable points in the leaves of different species, shows considerable diversity within the genus. The size of both the vascular bundles of the midribs and the conducting elements composing them is likewise variable. Kuntze (*22*) reported the veins of *G. herbaceum* to be without bast, but Heim de Balsac's (*14, v. 3*) diagrammatic sketch of the midrib of this species showed groups of pericyclic fibers. The veins of most species of *Gossypium* commonly lack fibers at the outer edge of the phloem throughout the greater part of their length. However, it is not unusual to find a few bast fibers capping the phloem toward the base of the larger veins. In large veins (pl. 4, *G*) the vascular bundles or fibrovascular bundles are surrounded by parenchyma which extends to a collenchymatic layer of variable thickness underlying the epidermis, while in small veins the parenchyma extends to the epidermis. Druses, probably of calcium oxalate, are often present in the parenchyma of both large and small veins. Lysigenous cavities resembling those occurring in the mesophyll are frequently present in the parenchyma of large veins (pls. 4, *F*; 5, *A*). Mucilage canals, such as are present in the parenchyma of the veins of species of *Hibiscus* (pl. 4, *D, E*), are apparently absent in *Gossypium*. As shown in plate 4, *D* and *E*, mucilage canals may occur in vein parenchyma above as well as below the vascular bundles, where they were observed by Kuntze (*22*).

NECTARIES

Nectaries are usually a conspicuous structural feature of the leaves of *Gossypium*, but they are apparently always lacking in *G. tomentosum* and are often absent in individual leaves or plants of other species. Unlike the extrafloral nectaries described by Tyler (*47*) as characteristic of one or both sets of involucres in *Gossypium*, the leaf nectaries are considered by Lewton (*23*) to be of little value in classification.

The leaf nectaries of *Gossypium* occur on the lower surface of from one to five major veins, being most common on the midrib. Only one nectary occurs on a vein, and it is usually close to the base of the vein in most species, but in *G. kirkii* it is characteristically well above the middle of the vein. Leaf nectaries vary considerably in size within

each of the three main groups of species. Nectary size does not always correspond to leaf size, the nectaries of *G. sturtii* being very long in proportion to leaf length, and those of hybrids involving the eglandular species *G. tomentosum* generally being very small in proportion to leaf size. Often the nectaries on major lateral veins are smaller than those on the midrib of the same leaf. Leaf nectaries likewise show wide variation in size in the close relatives of *Gossypium*, those of *Shantzia* being noteworthy because of their great length.

The leaf nectaries of *Gossypium* are most commonly rounded-triangular in outline, but may be nearly circular, elliptical, elongate-quadrangular, or sagittate, the shape showing no correlation with the main divisions of the genus. Cross sections taken at approximately the middle of nectaries (pl. 5, *A–I*) show that the extent of depression of the glandular surface, the size and shape of glandular hairs, and the contour of the sides of the nectaries are also variable.

Janda (*18*) recently classified the extrafloral nectaries of *Gossypium*, *Thespesia trilobata*, and *Cienfuegosia* as depressed nectaries, or nectaries with the secretory surface below the surrounding surface. In contrast, the nectaries of *Hibiscus rosa-sinensis*, *H. schizopetalus*, *H. archeri*, *H. syriacus*, and *Thespesia populnea* were classified as surface nectaries, or nectaries with the secretory surface lying at or near the same level as the surrounding epidermis; and the nectaries of *Kydia*, *Urena*, *Decaschistia*, *Dicellostyles*, *Julostylis*, and some species of *Hibiscus* were described as hollow nectaries, or nectaries with the secreting surface covering a cavity which has a small, slitlike orifice. Since Janda listed different species of *Thespesia* and *Hibiscus* as having different types of nectaries, it is not surprising that cross sections of some *Gossypium* nectaries (pl. 5, *C*, *D*) show that they might well be described as surface nectaries rather than depressed nectaries.

The ontogeny of the nectaries of cotton leaves has been traced by Schwendt (*39*, *pp. 254–256*) in *Gossypium brasiliense* and by Reed (*31*) in *G. hirsutum*. The histology of mature leaf nectaries of *G. brasiliense*, *G. herbaceum*, *G. davidsonii*, and *G. microcarpum* Tod. was compared by Schwendt (*39*), and the structure of leaf nectaries and involucral nectaries of *G. purpurascens* was compared by Janda (*18*). Although the leaf nectaries of different species of *Gossypium* vary in such characteristics as the size and number of glandular hairs, the number of simple or stellate hairs, and the size of cells composing their glandular and subglandular tissue, their general structure shows a marked similarity in all species. As in extrafloral nectaries discussed by Solereder (*43*), the upper, expanded portion of the glandular hairs of *Gossypium* nectaries is generally more strongly developed than that of capitate hairs of similar structure found elsewhere on the same plant (pl. 4, *G*, *H*). Bordering the glandular hairs of a nectary, the epidermal cells are often vertically elongate and are sometimes divided horizontally. Underlying the epidermis of the nectaries are several cell layers of subglandular tissue. As shown in plate 4, *G* and *H*, the cells of the subglandular tissue are smaller than the parenchyma cells of major veins outside the nectarial region. In some nectaries, druses of calcium oxalate are particularly abundant in the subglandular tissue.

PETIOLES

Within the genus *Gossypium* petioles of mature leaves vary greatly in size. According to Afzal (*1*) the petiole attains its full size at the

same time as the lamina, and there is a high correlation between length of petiole and length of midrib. There is also a general tendency for long petioles to be of greater diameter than short petioles, but individual exceptions to this generalization are of fairly common occurrence. The shape of a petiole in cross section depends considerably on the point in the petiole at which the section is taken (pl. 6, *D*, *E*, *F*). An indication of the range in size and shape of the midsections of petioles of *Gossypium* may be gained from plate 6, *A*, *B*, *C*, *E*, *G*, and *H*.

The epidermis of the petiole bears a marked resemblance to that of the major veins. The various types of epidermal hairs are well developed on the petiole and are often more conspicuous than on the midrib. Underlying the epidermis is a multicellular layer of collenchyma such as Plitt (*29*) described as characteristic of malvaceous petioles. The prominent ridges of the petioles of *G. kirkii* (pl. 6, *B*), which give them their quadrangular outline in cross section, are composed mostly of this tissue. Between the collenchyma and the well-developed fibers capping the phloem of the vascular bundles is a parenchymatic layer several cells deep. Oblate or spherical lysigenous cavities similar to those occurring in the parenchyma of veins are usually of scattered occurrence in this parenchymatic layer (*A–H*). At the midpoint of the petiole the fibrovascular system may take the form of a ring (*A*, *B*), an arc open at the top (*C*), or isolated bundles arranged in a ring (*E*). This diversity in arrangement of the vascular tissues of the petioles of *Gossypium* is greater than is indicated for the family Malvaceae by Dumont (*8*), Plitt (*29*), or Solereder (*43*).

While many species of *Gossypium* and related genera have dimorphic leaves (*3*), *G. thurberi* is notable for its diversity of leaf form. In this species the arrangement of the vascular tissues in cross sections taken at the midpoints of petioles of an entire leaf (pl. 6, *G*) and of leaves with two, three, four, and five lobes (*H*) showed but slight differences.

The central parenchyma of a petiole is usually homogeneous, although some of its cells frequently are conspicuous because of their dark-brownish contents (pl. 6, *A*). The central parenchyma of the petioles of the aberrant *G. kirkii* differs from that of the typical species of *Gossypium* examined in that it occasionally includes a few small medullary bundles and generally contains scattered spherical or oblate lysigenous cavities similar to those found in the lamina and in the cortex of the petiole (*B*). The occurrence of these cavities in the central parenchyma of the petiole of *G. kirkii* is of significance since Lewton (*23*) has pointed out that the distribution as well as the presence or absence of such cavities should be regarded as an anatomical character of value in classifying the Hibisceae.

EXPLANATORY LEGEND FOR PLATE 6.

Cross sections of *Gossypium* petioles and stems. *A–H*, Petioles (× 15): *A*, *B*, *C*, *E*, *G*, and *H*, Sections taken at approximately midpoint of petiole; *D*, section taken near top of petiole; *F*, section taken near base of petiole; *A*, *G. brasiliense*; *B*, *G. kirkii*; *C*, *G. armourianum*; *D–F*, *G. nanking*; *G*, *H*, *G. thurberi*. *I–O*, Stems (× 7½): *I–L*, very young stems; *M–O*, older stems; *I* and *M*, *G. purpurascens*; *J* and *N*, *G. arboreum*; *K* and *O*, *G. davidsonii*; *L*, *G. kirkii*.

STEM ANATOMY

SHAPE OF THE STEM AND ARRANGEMENT OF THE TISSUES

The stems of all species of *Gossypium* vary in cross-sectional shape at different stages in their development. As shown in plate 6, *I–L*, sections taken near the apices of the stems of Old World cottons, an American wild cotton, and a cultivated American cotton are angular and are generally inclined to be pentagonal in form. In contrast, sections of older stems (*M–O*) are rounded, often nearly circular, but sometimes broadly elliptic in outline.

The arrangement of the tissues in stems of *Gossypium* may be seen in plate 6, *I–O*, and plate 7, *A*, *B*, *C*, *E*. In centripetal order the primary permanent tissues (pl. 7, *B*) are epidermis, cortex merged with pericycle, phloem, cambium, xylem, and pith. In older stems the epidermis is underlain by periderm (*C*), which later replaces it (*E*).

EPIDERMIS AND PERIDERM

The epidermis of the stem is quite similar to that of the petiole The characteristic types of epidermal hairs are usually well developed near the apex of a stem but are less numerous where the epidermis is older. In a given plant, the capitate hairs near the apex of a stem are sometimes considerably larger than those over the green portions of the leaf blades, and approach those of the nectaries in size. A two-layered epidermis is present in the stems of some relatives of *Gossypium*, notably *Hibiscus splendens* (*24*) and *Alyogyne hakeaefolia* (pl. 7, *D*).

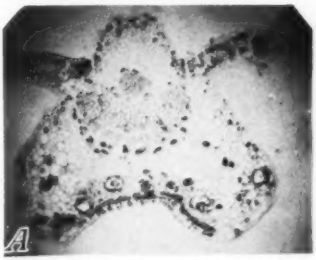
Periderm formation in the stems of *Gossypium* usually begins before the end of the first growing season. In numerous species of *Gossypium* the phellogen that gives rise to the periderm (pl. 7, *C*) forms in the outermost layer of cortical cells. A subepidermal phellogen is also characteristic of *Erioxylum aridum* and, according to Moeller (*27*), of *Hibiscus syriacus* L. and *Lavatera olbia* L. Solereder (*43*) reported that phellogen of epidermal origin is much less common in the Malvaceae, being known to occur only in the Ureneae, *Sida pulchella*, and most species of *Hibiscus*. At different ages the periderm of any given species is of rather different appearance. Different stages in the development of periderm in stems of *G. harknessii* are shown in plate 7, *C* and *E*. As has been reported by Kuntze (*22*), the phellem cells of most species of *Gossypium* often have brownish contents. The comparatively rare occurrence of oblate or spherical lysigenous cavities in the phelloderm of *Gossypium* stems has been discussed by Stanford and Viehoever (*45*).

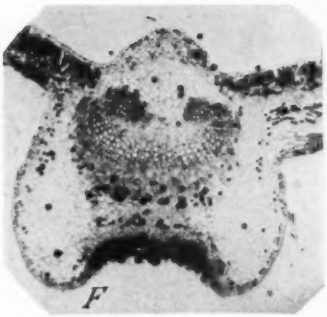
CORTEX AND PERICYCLE

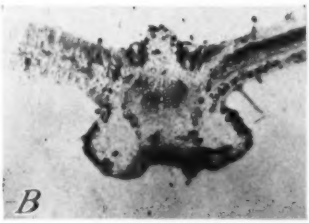
The general occurrence in the primary cortex of the stems of Malvaceae of an outer and an inner parenchymatous zone separated by a collenchymatous zone was reported by Solereder (*43*). These three

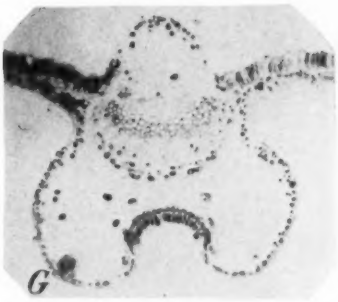
EXPLANATORY LEGEND FOR PLATE 7.

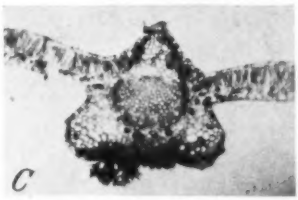
Stem sections. × 60. *A* and *D*, Stem epidermis and cortex: *A*, *Gossypium brasiliense*; *D*, *Alyogyne hakeaefolia*. *B*, *C*, *E*, *F*, *G. harknessii*; *B*, Young stem showing primary permanent tissues; *C*, somewhat older stem showing origin of periderm; *E*, somewhat older stem than *C*, showing replacement of epidermis by periderm and early stage in stratification of phloem; *F*, stratified phloem in old stem. *G* and *J*, *C. armourianum*, xylem showing lysigenous cavities in rays: *G*, Cross section; *J*, tangential section. *H*, *I*, *K*, and *L*, Cross sections of xylem showing differences in size and distribution of xylem elements within species: *H* and *I*, *G. africanum*; *K* and *L*, *G. hirsutum* var. Acala.

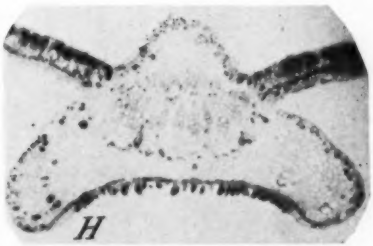


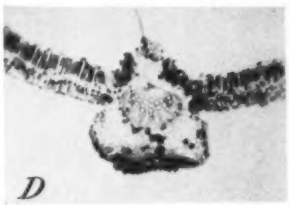


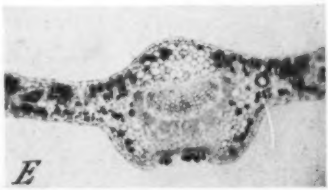


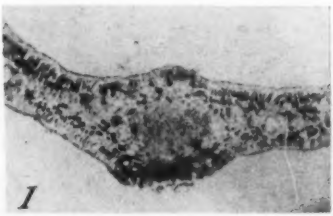




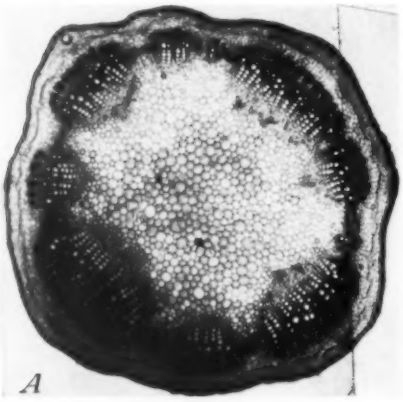


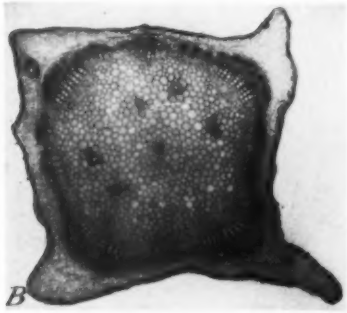


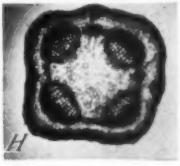


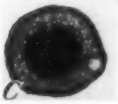


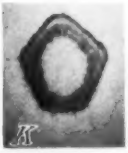
Cross sections of *Gossypium* leaf nectaries. × 25. *A, G. klotzschianum; B, G. nanking; C, G. herbaceum D, G. africanum; E, G. sturtii; F, G. darwinii; G, G. peruvianum; H, G. thurberi; I, G. harknessii.*

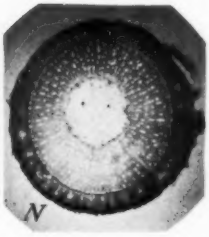


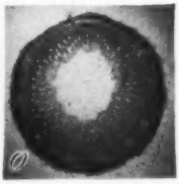












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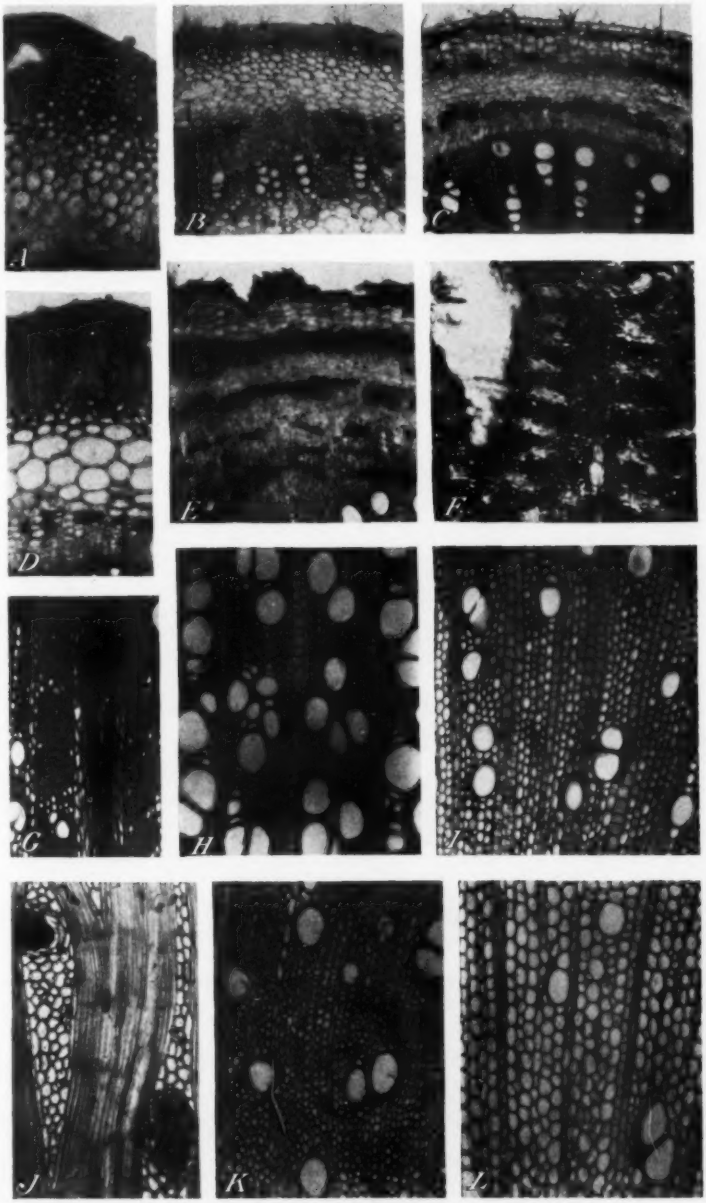

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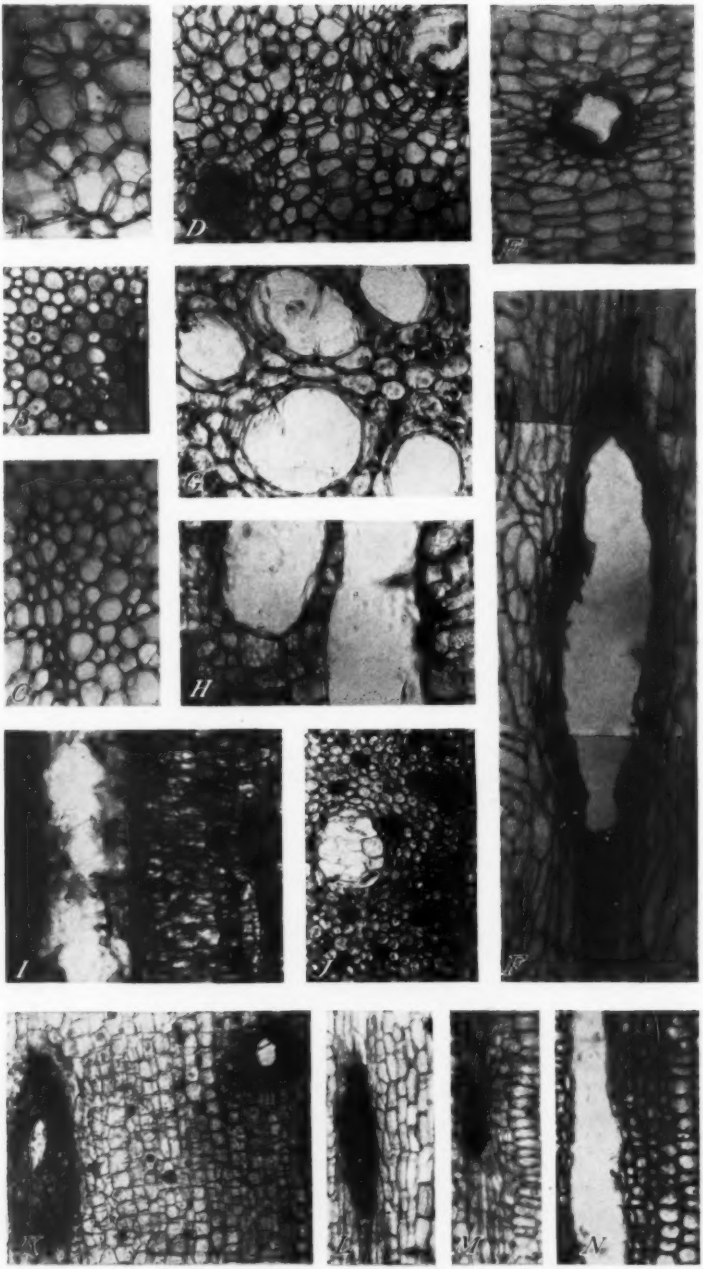

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zones are usually present in the cortex of stems of *Gossypium*, but, as shown in plate 7, *A* and *B*, they vary considerably in thickness and in the size and character of the cells composing them. Even greater variation in the characteristics of the three cortical zones is found in the Hibisceae. This may be seen by comparing the cortex of the stem of *Alyogyne hakeaefolia* (pl. 7, *D*) with that of species of *Gossypium*. Oblate or spherical lysigenous cavities, similar to those described in the leaves, were present in the cortex of all species of *Gossypium* examined. They occur in all three cortical zones, but are perhaps more common in the outer parenchymatous zone and the collenchymatous zone (*A*) than in the inner parenchymatous zone. This distribution of lysigenous cavities is in contrast to that of mucilage canals in related genera, which are reported (*8*) to occur in the outer parenchymatous zone only in the Eumalveae and are usually formed in the inner parenchymatous zone.

In *Gossypium* and related genera (pl. 7, *D*), pericyclic fibers are developed during the first year's growth of the stem. They show some differences in diameter and thickness of cell wall in stems of different ages (*B*, *C*), and perhaps among different species. They adjoin the phloem in groups of variable size (*B*, *C*, *E*).

PHLOEM AND XYLEM

Moeller (*27*) and Solereder (*43*) have called attention to the characteristic shape of the phloem portion of vascular bundles in the Malvaceae. As shown in plate 6, *M–O*, the phloem between the primary rays is considerably broader adjoining the cambium than at its outer edge, while in contrast the rays are broadened outward. Although Dumont (*8*) considered stratification of the phloem as one of the most characteristic features of the Malvaceae, he reported that this characteristic is obscure in the Hibisceae, and particularly so in the Gossypieae, because of the sparsity of phloem fibers, these being entirely absent in *Cienfugosia* (*Fugosia*). In the various species of *Gossypium* examined, the phloem is distinctly stratified (pls. 6, *M*; 7, *E*, *F*) in all but very young stems. The groups of fibers are, however, more conspicuous in some specimens than in others. The fairly common occurrence of oblate or spherical lysigenous cavities in the phloem rays of *Gossypium* has been noted by Stanford and Viehoever (*45*). According to Hawkins, Matlock, and Hobart (*13*), phloem growth in Acala cotton was stimulated by increased soil moisture, but to a lesser extent than was the xylem.

The xylem of the Hibisceae was described by Dumont (*8*) as very parenchymatous, with few but very large vessels. Webber's (*50*, *51*, *52*) descriptions of malvaceous woods indicate much more structural diversity in the woods of this tribe. A difference in porosity or compactness of the wood of Old World and New World cottons was reported by Zaitzev (*54*). As shown in plate 7, *H*, *I*, *K*, *L*, woods of both Old World and New World cottons often show wide variation

Sections of pith. × 60. *A*, *B*, *C*, Cross sections of pith without lysigenous cavities or mucilage canals: *A*, *Gossypium peruvianum*; *B*, *G. armourianum*; *C*, *G. neglectum*. *D*, *E*, *F*, *G. kirkii*, showing variation in size and form of lysigenous cavities in pith: *D*, Cross section; *E* and *F*, longitudinal sections. *G* and *H*, *Hibiscus brackenridgei* showing mucilage canals in pith: *G*, Cross section; *H*, longitudinal section. *I* and *J*, *Thespesia lampas*, pith showing nearly spherical lysigenous cavities with dark contents and mucilage canals: *I*, Longitudinal section; *J*, cross section. *K*, *Kokia drynarioides*, longitudinal section showing lysigenous cavities of different forms in pith. *L*, *Eriorytum aridum*, longitudinal section showing elongated lysigenous cavity in pith. *M* and *N*, *Shantzia garckeana*, longitudinal sections of pith: *M*, Showing lysigenous cavity with dark contents; *N*, showing mucilage canal.

in size of the xylem elements and abundance of vessels. Although Stanford and Viehoever (*45*) failed to find oblate or spherical lysigenous cavities in the xylem of *Gossypium*, they were noted by Webber (*52*) in the xylem rays of *G. mexicanum*, *G. morrilli*, *G. peruvianum*, and *G. schottii*. They are also of frequent occurrence in the xylem rays of *G. armourianum* (*G*, *J*). As reported by Dumont (*8*), reddish-brown contents are often abundant in the ray cells and wood parenchyma of the xylem of *Gossypium*.

PITH

The pith of *Gossypium* is entirely parenchymatous, lacking the stone cells and sclerenchyma fibers reported by Solereder (*43*) as characteristic of some Malvaceae. Within a single species the cells vary considerably in size, wall thickness, and contents at different stages in their development. Comparable differences occur between mature pith cells of different species (pl. 8, *A*, *B*, *C*). The pith of *Alyogyne hakeaefolia* resembles that of *Gossypium*, and according to Mentovich (*26*) the pith is homogeneous in *Hibiscus syriacus* and *H. sinensis*. Although scattered cells with yellowish or brownish contents are common in all species of *Gossypium*, lysigenous cavities with brownish contents were observed within the genus only in the very aberrant *G. kirkii* (pl. 8, *D*, *E*, *F*). Similar cavities occur also in the pith of the related species *Erioxylum aridum* (*L*), *Shantzia garckeana* (*M*), *Kokia drynarioides* (*K*), and *Thespesia lampas* (*I*, *J*). Although the lysigenous cavities in the pith of *G. kirkii* and *Erioxylum aridum* are often spherical or nearly so (*E*), they are at times much more vertically elongate (*F*, *L*) than those observed elsewhere in the stems and leaves of *Gossypium* and related genera. Some of these elongate cavities might be regarded as short ducts or canals. They are, however, considerably shorter than most of the mucilage canals occurring in the pith of *Lagunaria patersonii*, *Hibiscus brackenridgei* (*G*, *H*), *Thespesia lampas* (*I*, *J*), *Kokia drynarioides*, and *Shantzia garckeana* (*N*). According to Dumont (*8*), who discussed the distribution of mucilage canals in the Malvaceae, such ducts are abundant in the Eumalveae, Sideae, and Malopeae, but comparatively rare in the Hibisceae. Within the latter tribe he observed them in *Hibiscus splendens*, *H. cameroni*, and *H. palustris*.

DISCUSSION

A histological examination of the leaves and stems of Old World cottons ($n=13$), American wild cottons ($n=13$), and New World cultivated cottons ($n=26$), has shown that within each of these groups there is considerable variation in certain structural characteristics that have hitherto been suggested as valuable in distinguishing between Old World and New World cottons. It seems probable that some of the reports of distinctive characters for the different groups were based on superficial examination of specimens or on the examination of too limited a collection of specimens to warrant the generalizations that were made.

The type of pubescence has been suggested by Zaitzev (*54*), who excludes the wild American cottons with 13 pairs of chromosomes from the genus *Gossypium*, as a means of distinguishing between Old World and New World cottons. He listed among distinctive morpho-

logical characteristics of the two groups the universal absence in New World cottons of a "two-layered pubescence,—i. e., pubescence of long and short hairs" and the occasional presence of this character in Old World species. This distinction is very misleading since it is applicable only to macroscopic stellate hairs and simple hairs and not to minute capitate or glandular hairs, which appear to be present throughout the genus, even on leaves often described as entirely glabrous. When the presence of the short capitate hairs is considered, the pubescence of New World cottons is seen to be always two-layered and that of the Old World cottons sometimes three-layered.

Aside from the nature of the pubescence, no epidermal character has been found that may be used to distinguished any of the main groups of *Gossypium*. Although there is considerable diversity in epidermal structure within the genus, none of the structural features, such as relative number of stomata on the upper and lower surfaces of the leaf, size and shape of stomata, level of the guard cells in relation to that of ordinary epidermal cells, or relative size and shape of the ordinary epidermal cells on the upper and lower leaf surfaces, is of value in delimiting the main groups of species, as there is considerable variation in each of these characteristics within every group.

Although Magitt and Magitt (*25*) did not include American wild cottons in their study, they reported the distribution of palisade tissue as differing in the leaves of Old World and New World cottons. Nevertheless, species with bifacial leaves and with subcentric to centric leaf structure occur within each of the three groups. The distribution of palisade tissue in the leaves of American wild cottons is of particular interest in view of Skovsted's (*42*) report on the relationships within the group. He considered *Erioxylum aridum*, which he renamed *Gossypium aridum*, *G. thurberi* (*20*), *G. armourianum*, and *G. harknessii* to be more closely related to one another than to *G. davidsonii* and *G. klotzschianum*. While the mesophyll of *G. armourianum* resembles that of *G. harknessii* in having well-developed palisade tissue on both sides of the leaf, the mesophyll of *G. thurberi* and *Erioxylum aridum*, which are also natives of dry areas, resembles that of *G. davidsonii* and *G. klotzschianum* in having spongy parenchyma adjacent to the lower epidermis of the leaf.

The shape of the stems in cross section is one of the characters enumerated by Zaitzev (*54*) as useful in distinguishing between Old World and New World cottons. He states that the cross section of the stem is circular in cottons of the Old World group, but oval or angular in New World cottons. This statement was evidently based on an examination of stems of different ages. As shown in plate 6, *I–L*, the stems of cottons belonging to both groups discussed by Zaitzev, and of American wild cottons as well, are angular, usually pentagonal in cross section near their apices. As the stems grow older they lose their angularity. Cross sections of 1-year-old and older stems are usually oval or nearly circular, and are often more nearly circular in New World than in Old World species. A "square stem" is listed by Skovsted (*41*) among the characteristics that distinguish *Gossypium kirkii*, the type of his genus *Gossypioides*, from most of the species of *Gossypium*. As shown in plate 6, *L*, very young stems of *G. kirkii* are star-shaped in cross section. As the stems grow older they become less noticeably ridged and nearly pentagonal in

cross-sectional outline. In view of the widespread occurrence of a similar shape in the sections of young stems of other species of *Gossypium*, the stem shape of *G. kirkii* is less peculiar than Skovsted considered it to be. It should, however, be pointed out that the stems of *G. kirkii* retain their angularity longer than those of more typical species of *Gossypium*.

In view of the reported (*43*) epidermal origin of phellogen in most species of *Hibiscus* and the subepidermal origin of phellogen in *Gossypium*, determination of the place of origin of phellogen in *G. kirkii* might have some taxonomic bearing. Skovsted (*41*) has shown that this species in some respects resembles *Hibiscus* rather than *Gossypium*. Unfortunately the origin of the phellogen cannot be determined in material of this species now available.

Zaitzev (*54*) considered the xylem structure of Old World and New World cottons as sufficiently distinct to be useful in distinguishing between the two groups. He described the wood of Old World cottons as "compact" and that of New World cottons as "porous." This terminology is confusing in view of the technical terms used in describing wood (*17*). The woods of all species of *Gossypium* are "porous" in the sense that they have pores, i. e. vessels in cross section. Accordingly Zaitzev's (*54*) descriptions of differences in porosity of the woods of different groups of *Gossypium* might be interpreted to refer to differences in the number of vessels only, but it seems probable that they refer instead to differences in texture, which is dependent on the size of wood elements. Regardless of whether difference in vessel number or difference in size of various wood elements was meant by Zaitzev, his distinction between the woods of Old World and New World cottons is not valid. As shown in plate 7, *H*, *I*, *K*, *L*, the woods of both New World and Old World cottons are diffuse-porous, but the number of pores in a unit of area and the size of the various wood elements are often highly variable in the same stem. Hawkins, Matlock, and Hobart (*13*) have shown that the size of the wood elements and the thickness of their walls in Acala cotton (*G. hirsutum*) are influenced by available soil moisture.

The presence and distribution in the Hibisceae of oblate or spherical lysigenous cavities filled with brownish contents was regarded by Lewton (*23*) as a valuable characteristic in classifying this group. It is therefore noteworthy that such cavities may occur in xylem rays, central parenchyma of petioles, and pith of stems, in addition to the tissues in which their occurrence was reported by Stanford and Viehoever (*45*). In the pith of *G. kirkii*, in addition to the common oblate or spherical lysigenous cavities (pl. 8, *E*), various transitional forms to short, canallike cavities with dark contents occur (*F*). Both typical oblate or spherical cavities and typical mucilage canals occur in the pith of *Kokia*, *Shantzia*, and *Thespesia*. Dumont's (*8*) distinction between Euhibisceae with mucilage canals and Gossypieae with spherical cavities is therefore invalid.

The presence of lysigenous cavities in the pith of the stems and petioles of *G. kirkii* and their absence in all other species of *Gossypium* examined is of significance, since, for cytological reasons, the inclusion of this species in the genus *Gossypium* has been questioned (*41*). This characteristic may therefore be considered as further grounds for excluding this species from the genus *Gossypium*. Since Skovsted

(*41*) has noted the resemblance of *G. kirkii* to the *Hibiscus* subtribe as well as to the *Gossypium* subtribe, the presence in this species of both spherical lysigenous cavities such as are common in *Gossypium* and elongated cavities approaching the form common in *Hibiscus* is of interest.

Erioxylum aridum has been referred to the genus *Gossypium* on cytological grounds (*41*, *42*). It should therefore be noted that lysigenous cavities such as occur in the pith of *Erioxylum* (pl. 8, *L*) are not characteristic of the pith of *Gossypium*, although they occur in other tissues in the latter genus.

SUMMARY

The descriptions of leaf and stem structure of *Gossypium* presented in this paper are based on a histological examination of the leaves and stems of 12 Old World species, 5 wild American species, 10 cultivated or semiwild American species, 2 doubtful species, and 9 species belonging to related genera.

There is more anatomical variation within each of these three groups, and less between the several groups, than previous descriptions indicated.

Since the distribution of spherical or oblate lysigenous cavities has been thought to be of value in classifying the Hibisceae, their hitherto unreported occurrence in the xylem rays of *G. armourianum* and in the pith of *G. kirkii*, *Erioxylum aridum*, *Kokia drynarioides*, *Shantzia garckeana*, and *Thespesia lampas* is significant.

The presence of both spherical lysigenous cavities and elongate mucilage canals in the pith of *Kokia*, *Thespesia*, and *Shantzia* is of interest since the type of cavity present in either cortex or pith has been suggested as a means of distinguishing between the subtribes Euhibisceae and Gossypieae of the tribe Hibisceae.

The occurrence of spherical to elongate lysigenous cavities in the pith of *G. kirkii* may be considered as an additional reason for excluding this species from the genus *Gossypium*, since no such cavities were observed in the pith of typical species of *Gossypium*.

In regard to Skovsted's proposed inclusion of *Erioxylum aridum* in the genus *Gossypium*, it should be pointed out that this species differs from all typical species of that genus that were examined in having lysigenous cavities in its pith.

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TWO MASTIGOSPORIUM LEAF SPOTS ON GRAMINEAE[1]

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INTRODUCTION

The type species of the moniliaceous genus *Mastigosporium* Riess is *M. album* Riess (*6, p. 56*)[3], which attacks a number of grasses in Wales, France, central Europe, the Union of Soviet Socialist Republics, and Scandinavia (*9, 10, 11, 15*). The fungus is distinguished by the presence of one to several tentaclelike appendages extending from the awl-shaped distal end of its hyaline, elliptical, three-(three-to-five) septate conidia (figs. 1, *J-O*, and 2).

The writer recognized a second species of *Mastigosporium*, which has nonappendaged conidia (fig. 1, *a-i*). The fungus, *M. calvum* (Ellis and Davis) comb. nov., occurs in Germany (*5*), France (*14, p. 254*), England (*16, p. 233*), Wales, Russia (*1*), Ontario, Canada, and in Wisconsin (*3, p. 98*), Montana (*4, p. 361*), and Oregon.[4]

Most of the present study deals with *Mastigosporium calvum*, as it is conveniently abundant in western Oregon. *M. album* apparently has not been found in North America.

DISTRIBUTION AND ECOLOGY OF MASTIGOSPORIUM CALVUM IN THE WESTERN UNITED STATES

The disease caused by *Mastigosporium calvum* is the most important malady of orchard grass (*Dactylis glomerata* L.) in portions of western Oregon. It is common in the northern end of the Willamette Valley from Benton County north to at least the Columbia River and east through the Columbia Gorge into Hood River County. It is prevalent on orchard grass in the coast region from Astoria, south to Lane County, which is as far south as observations were made. In commercial fields of seed grass in Clatsop County the disease is prevalent on redtop (*Agrostis alba* L.). In 1937 it was also very abundant on the locally more important Astoria colonial bent (*A. tenuis* Sibth.) in Clatsop and Tillamook Counties. Scattering infection occurs on creeping bent (*A. palustris* Huds.) in commercial bentgrass seed fields in Clatsop County and is common in pastures in Lincoln County.

The apparent susceptibility of a number of grasses is shown in table 1. These data were compiled from rod-row plots at Astoria, Oreg. All the grasses were the same age and were growing side by side in the

[1] Received for publication February 4, 1938; issued August 1938. Cooperative investigations by the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, and the Oregon and Washington Agricultural Experiment Stations. Published as Technical Paper No. 270 of the Oregon Agricultural Experiment Station.

[2] The writer is indebted to A. G. Johnson and John A. Stevenson for more than routine aid in locating material and literature; to A. G. Johnson for a critical revision of the manuscript; and to John H. Martin for translating Bondarzeva-Monteverde's article from the original Russian.

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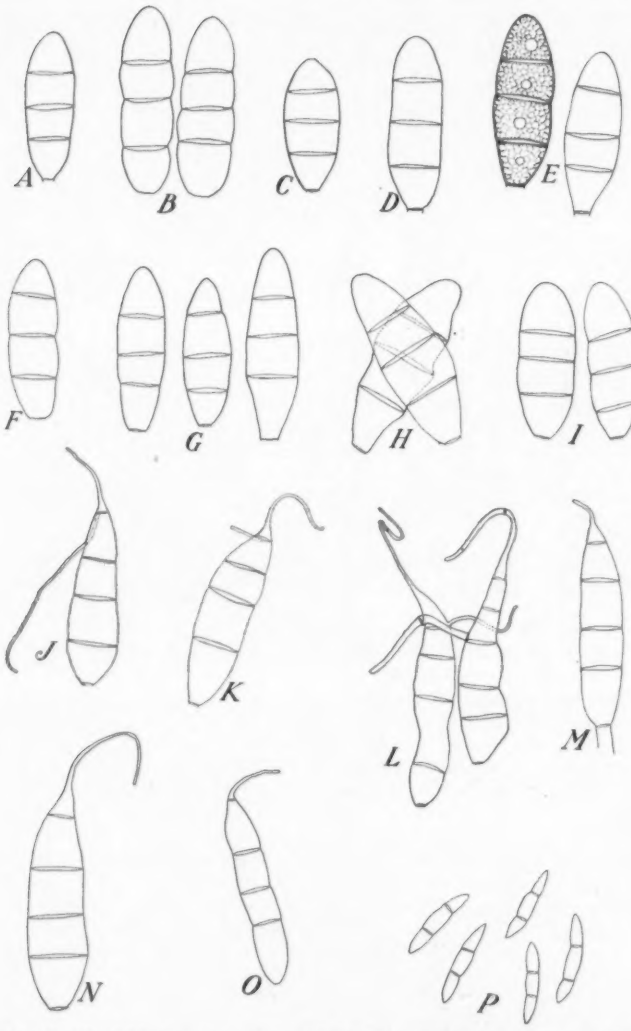

FIGURE 1.—Conidia of *Mastigosporium calvum*, *A-I*; *M. album*, *J-O*; and *Septogloeum athrix*, *P*. From following sources: *A*, On *Agrostis alba*, Astoria, Oreg., Oregon 10386; *B*, on *A. palustris*, Big Elk Creek, Lincoln County, Oreg., Oregon 8246; *C*, on *A. palustris*, Alsea Valley, Oreg., Oregon 10308; *D*, on *A. tenuis* var., Astoria, Oreg., Oregon 10585; *E*, on *Calamagrostis canadensis*, Ontario, Canada, Univ. Toronto. Crypt. Herb., 1292; *F*, on *C. canadensis*, State Line, Wis., 1903, Univ. Wis., J. J. Davis Herb.; *G*, on *C. canadensis* var. *scabra*, Glacier Park, Mont., type of *Fusoma rubricosa*, Fungi Columb., 5019; *H*, on *C. epigeios*, Germany, Sydow, Myc. Ger., 640; *I*, on *Dactylis glomerata*, Germany, Krieger, Fungi Sax., 792; *J*, on *Alopecurus pratensis*, Germany, Sydow, Myc. Ger., 542; *K*, on *Alopecurus pratensis*, Germany, Krieger, Fungi, Sax., 790A; *L*, on *A. pratensis*,[1] Germany, Krieger, Fungi Sax., 790B; *M*, on *A. pratensis*, Bohemia, Kabát and Bubák, Fungi Imp. Exs., 386; *N*, on *A. pratensis*, Russia, Buchholz et Bondarzew, Fungi Ross. Exs., Ser. A, 197; *O*, on *Deschampsia caespitosa*,[2] Germany, De Thümen, Myc. Univ., 1872; *P*, on *Calamagrostis* sp., Sweden, Eriksson, Fungi Par. Scand., 394. All × 667.

[1] This collection has a number of conidia with very robust appendages that have all the appearances of germ tubes.

[2] This collection has spores badly plasmolyzed.

rows. Infection was heavy in 1937. On redtop, for example, nearly 100 percent of the leaves had at least one spot and most of them had several. The same relative susceptibility had been noted in 1936.

In Benton, Linn, Polk, Marion, Clackamas, Multnomah, and Lincoln Counties, Oreg., the fungus recurs annually on the same

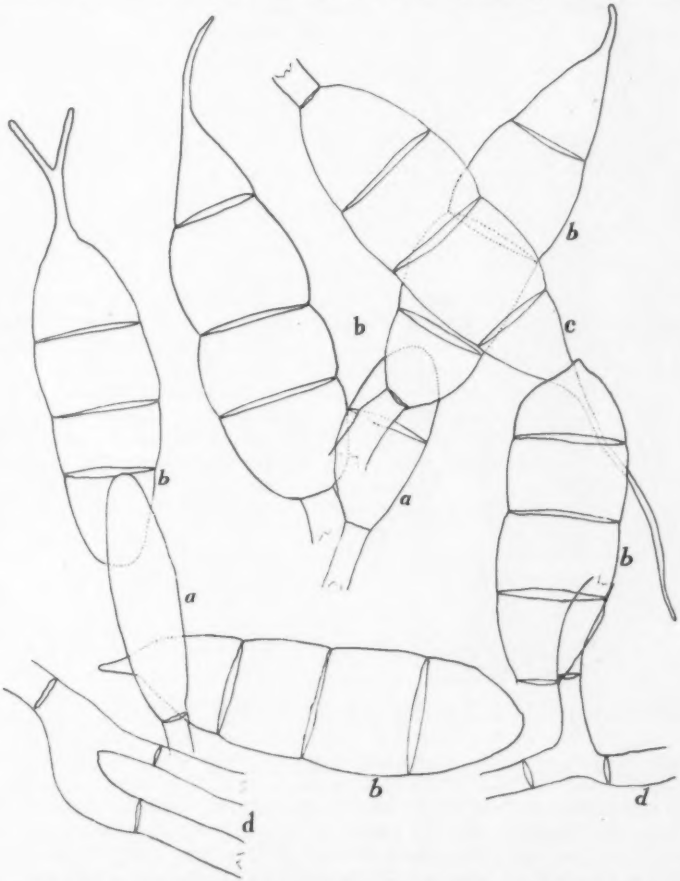

FIGURE 2.—Conidia of *Mastigosporium album* from *Alopecurus pratensis* sent by K. Sampson from Aberystwyth, Wales, April 1937, showing unplasmolyzed condition: *a*, Young conidia with attached conidiophores; *b*, maturing conidia; *c*, nearly mature conidium; *d*, fragments of hyphae. All × 1,375.

plants of orchard grass. The disease very largely disappears during the summer, but after rains start in the autumn it appears again following periods of growing weather. The disease has been most evident during February, March, and April. In the very humid coastal counties of Lincoln, Tillamook, and Clatsop the disease has continued to develop later in the spring than elsewhere, the lateness of development depending largely on the seasonal prevalence of rains. The fungus is evidently soon checked by low humidity.

TABLE 1.—*Relative susceptibility to Mastigosporium calvum of certain grasses grown under humid field conditions in the plots at the John Jacob Astor Experiment Station, Astoria, Oreg., as indicated by observations made May 12, 1937*

Host		Relative susceptibility
Technical name	Common name	
Agrostis alba L.	Redtop	Completely susceptible.
A. canina L.	Velvet bent	Susceptible.
A. palustris Huds.	Creeping bent	Do.
A. stolonifera L.	do	Moderately susceptible.
A. tenuis Sibth.	Astoria colonial bent	Very susceptible.
A. tenuis Sibth.	Rhode Island colonial bent	Susceptible to very susceptible.
A. tenuis var.	Highland colonial bent	Do.
A. verticillata Vill.	Water bent	Slightly resistant.
Alopecurus pratensis L.	Meadow foxtail	Apparently immune.
Arrhenatherum elatius (L.) Mert. and Koch.	Tall oatgrass	Do.
Dactylis glomerata L.	Orchard grass	Susceptible.
Lolium perenne L.	Perennial ryegrass	Apparently immune.
Phleum pratense L.	Timothy	Do.

Fusoma rubricosa Dearn. and Barth., which, as shown later, is the same fungus as *Mastigosporium calvum*, was collected on *Calamagrostis scabra* Presl from Glacier National Park, Mont., in August 1915 (*4*). The host, which is now generally known as *C. canadensis* var. *scabra* (Presl) Hitchc., is a plant of subalpine and alpine areas in the northern United States and Canada. It is interesting to note that Frank (*5*) found a muticate form of *M. album* on *Alopecurus pratensis* on the highest parts of the Erzgebirge of Saxony, Germany. In commenting on this, Lindau (*10*) wondered whether the muticate spores were due to the altitude or to a species difference. It is noted in Oregon that most of the collections of *M. calvum* have been made at elevations between 0 and 400 feet above sea level. Whether or not *M. calvum* occurs on alpine and subalpine grasses in Oregon has not been determined.

SYMPTOMS CAUSED BY MASTIGOSPORIUM CALVUM

SYMPTOMS ON DACTYLIS GLOMERATA

The disease caused by *Mastigosporium calvum* on *Dactylis glomerata* is first visible as small, dark, purple-brown flecks on the leaves. Some of these enlarge, becoming elliptical in outline, with ashy-gray to fawn-color centers. The lesions measure 1 to 8 mm in length and are somewhat restricted by the parallel veins of the leaf (fig. 3). Where the fungus is able to make rapid headway or where secondary infection from spores occurs the lesions may be larger, somewhat mottled, and with less definite borders. These larger lesions show various shades of gray, ashy, or light-fawn color, with more or less definite purple, red, or ocher borders. Any or all leaves of a plant may be attacked, as the fungus is an active parasite and may practically defoliate the orchard grass plants.

The presence of long, dead striae, with black dots of conidiophore tufts, is indicative of the presence of the streak disease caused by *Scolecotrichum graminis* Fckl., which is frequently associated with the mastigosporium disease in Oregon. The symptoms of the streak disease, which are well described by Horsfall (*7*), are sometimes confusable with those of the mastigosporium leaf spot. The purple

flecking mentioned for the latter is sometimes duplicated in early stages of the streak disease. Usually, however, *Mastigosporium calvum* causes a more abundant development of pigments than does *S. graminis*, and, furthermore, the latter produces longer lesions, usually with rather conspicuous black tufts of conidiophores.

SYMPTOMS ON AGROSTIS SPECIES

The symptoms produced by *Mastigosporium calvum* on *Agrostis* spp. differ from those on orchard grass in the tendency to form broader, elliptical, light-brown lesions with light-fawn centers. The lesions are often of an eyespot or frogeye type on account of a broad red or red and yellow margin. On redtop the lesions were sufficiently numerous to destroy most of the leaves of plants in certain fields near Astoria in 1936 and1937. On Astoria colonial bent the spots averaged from one to six per leaf with a tendency to develop at the tips or where moisture collected at the base of the leaf blades. In 1937 colonial bent was heavily infected during April and May in Clatsop and Tillamook Counties.

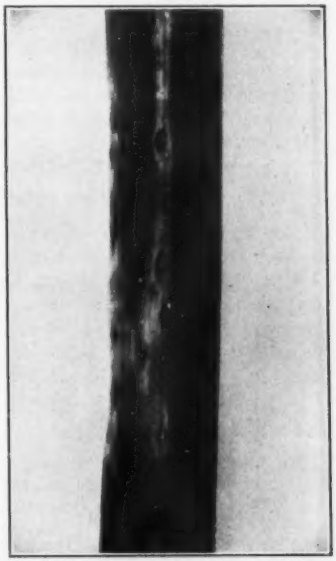

FIGURE 3.—Leaves of *Dactylis glomerata* attacked by *Mastigosporium calvum*, Corvallis, Oreg. × 2.

SYMPTOMS ON CALAMAGROSTIS SPECIES

On species of *Calamagrostis*, *Mastigosporium calvum* produces small brown flecks, 1 to 3 mm in diameter, with very small gray centers. The entire lesion is sometimes surrounded by larger areas of fawn- or pale buff-colored tissue. Specimens from Montana showed extensively coalesced, mottled lesions.

SYMPTOMS CAUSED BY MASTIGOSPORIUM ALBUM IN EUROPE

While field comparisons have not been made, it is doubtful whether *Mastigosporium calvum* and *M. album* can be readily distinguished in the field except possibly by hosts. *M. album* is the more common, in exsiccati at least, on *Alopecurus pratensis* and *Deschampsia caespitosa* (L.) Beauv., while *M. calvum* prefers *Dactylis glomerata*, *Agrostis* spp., and *Calamagrostis* spp. Lindau (*10*), however, lists a number of hosts other than these for *M. album*. Since he has not distinguished entirely between the muticate and nonmuticate collections, and since these collections are not available to the writer, it is not possible to give a more extensive host range. Lindau lists, in addition to the ones cited, *Brachypodium sylvaticum* (Huds.) Beauv., *Molinia caerulea* (L.) Moench, *Avena elatior* L., *Briza media* L., *Glyceria fluitans* (L.) R. Br., *Holcus lanatus* L., *H. mollis* L., *Phleum pratense* L., *Poa trivialis* L., and *Trisetum flavescens* (L.) Beauv.

The following notes on symptoms are based on an examination of exsiccati and a study of the brief reports in literature.

SYMPTOMS ON ALOPECURUS PRATENSIS

On *Alopecurus pratensis* there usually are numerous small elliptical purple-brown to dark-brown flecks which later enlarge and develop white to ashy-gray centers. The coloration on *A. pratensis* is deeper than for most collections of *Mastigosporium calvum* on *Dactylis glomerata*, but this probably is attributable as much to host reaction as to differences in the two fungi.

SYMPTOMS ON DESCHAMPSIA CAESPITOSA

On *Deschampsia caespitosa* (*Aira caespitosa* L.) the symptoms are very similar to those on *Alopecurus pratensis* except that the spots on the former grass seem to be slightly less deeply pigmented than those on the latter, as indicated by the specimens in De Thümen, Myc. Univ., 1872.

PURE-CULTURE STUDIES

MASTIGOSPORIUM CALVUM FROM DACTYLIS GLOMERATA

Pure cultures of *Mastigosporium calvum* were obtained from spores washed from leaves of orchard grass collected at Corvallis, Oreg. The fungus, which grows relatively slowly on potato-dextrose agar, produces a leathery, somewhat folded and mounded colony which becomes pebbly or roughened by the formation of small, partially embedded, stromatic or sclerotic mycelia that resemble pycnidia. Brief descriptions of the development of the fungus during the first month after transfer of diseased host tissue to four kinds of nutrient media are given in table 2.

TABLE 2.—*Development of mycelia of Mastigosporium calvum on four kinds of nutrient agar at 35° to 40° F. in total darkness*

Agar culture medium	Color of—		Description of colony
	Substratum	Aerial mycelia	
Difco corn decoction	Yellow	Straw, later yellow	Stellate-margined, leathery wrinkled colonies, partially submerged.
Mix's synthetic	White	White	Flat, thin, spreading colonies.
Difco potato dextrose	Pale umber	Tan to fawn	Leathery, pebbly mounded, wrinkled colonies.
Difco prune	Pale cocoa	Pale cocoa to fawn	Less mounding, margins more stellate.

Normal-appearing conidia were produced in moderate quantities on the surface of the colonies on potato-dextrose agar after incubation for several weeks in the ice box at 35° to 40° F. After growing several months at this temperature the colonies finally became orange brown and the sclerotia increased in number, frequently forming rings in the substratum around the original point of transfer.

MASTIGOSPORIUM CALVUM FROM AGROSTIS SPECIES

Pure cultures of *Mastigosporium calvum* were isolated from *Agrostis alba*, *A. canina*, and *A. tenuis* collected at Astoria, Oreg.

MASTIGOSPORIUM CALVUM FROM ALOPECURUS

A culture of *Mastigosporium album* from *Alopecurus pratensis*, kindly forwarded by Kathleen Sampson from Aberystwyth, Wales,

had the same general yellow-brown color of *M. calvum* but produced masses of conidia in glistening orange-brown mounds on the surface of the colony. After transfer to potato-dextrose agar the sporulation continued but was at first putty-colored, later darker. The conidia were typically navicular, three- to five-septate, and bore the characteristic appendages at the apex. The fact that this fungus continues to produce typical conidia in culture that do not revert to the muticate type is additional strong evidence that the muticate and ciliated species are distinct.

DILOPHOSPORA ALOPECURI FROM HOLCUS LANATUS

Since Rainio (*11*) has strongly contended that *Mastigosporium album* is an early stage of *Dilophospora alopecuri* (Fries) Fries, the writer isolated cultures of the latter fungus from *Holcus lanatus* from Oregon. This fungus grew very slowly, and germinating spores required nearly 8 weeks to produce macroscopically visible colonies when incubated at 38° F. After 6 months the colony covered the surface of test-tube slants with a mounded, felty, olive and gray growth, which was covered with guttulae. These cultures, therefore, differed distinctly from those of *M. calvum*.

INOCULATION STUDIES

Water suspensions of viable conidia of *Mastigosporium calvum* taken from naturally infected plants in the field were sprayed with an atomizer on pot-grown, healthy grasses in the greenhouse at Corvallis. The inoculated plants, together with adequate checks, were incubated in a moist chamber for 1 week. The first series, conducted in January 1934, and a second series, conducted the following month, produced a light infection on orchard grass only. Another more extensive series of inoculations was conducted in May 1937 with *M. album* from Wales and with spore washings of *M. calvum*, both from *Dactylis glomerata* and *Agrostis alba*. The results are shown in table 3.

TABLE 3.—*Results of inoculating grasses in the greenhouse with spore suspensions of Mastigosporium album and M. calvum*

Host	Inoculated with *M. album* from *Alopecurus pratensis*, May 1, 1937		Inoculated with *M. calvum* from—							
			Dactylis glomerata						*Agrostis alba*, May 1937	
			January 1934		February 1934		May 1937			
	Leaves infected	Leaves not infected	Leaves infected	Leaves not infected	Leaves infected	Leaves not infected	Leaves infected	Leaves not infected	Leaves infected	Leaves not infected
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Agrostis palustris Huds.	0	190					0	400	10	265
A. tenuis Sibth.	0	175					0	215	78	65
Alopecurus pratensis L.	38	46					0	80	0	240
Avena sativa L.					0	48	0	90	0	98
Brachypodium pinnatum (L.) Beauv.	6	30								
Bromus rigidus Roth.	0	15							0	120
Dactylis glomerata L.	0	205	5	206	39	180	31	0	10	290
Deschampsia caespitosa (L.) Beauv.	16	227					0	165	0	190
Festuca elatior L.	0	150								
F. rubra L.					0	60				
Holcus lanatus L.	0	51			0	84	0	88	0	155
Lolium perenne L.			0	63	0	79	0	100	0	180
Phleum pratense L.	0	40								
Poa pratensis L.	0	75	0	52	0	75	0	85		
Triticum aestivum L.	0	36			0	45	0	25		

It will be noted that *Mastigosporium album* from *Alopecurus pratensis* attacked that host, *Brachypodium pinnatum*, and *Deschampsia caespitosa; M. calvum* from *Dactylis glomerata* attacked only that host, and this fungus from *Agrostis alba* attacked *A. palustris*, *A. tenuis*, and *D. glomerata*.

While further inoculations are needed, the present results indicate (1) that *Mastigosporium album* and *M. calvum* differ in host range as well as in morphology, and (2) that there are distinct physiologic races in *M. calvum*.

MORPHOLOGY OF MASTIGOSPORIUM CALVUM

In pure cultures of *Mastigosporium calvum* the conidia are produced on the tips of hyphae (fig. 4). The distal portions of the conidia, following the constriction at the base of the conidiophore, develop faster than the basal portions. In the young conidium there are two nuclei which divide and form four cells in the mature spore. The four-celled condition is typical and is remarkably uniform. Sometimes spores with only two cross walls are found, but these are immature spores with the basal portions incompletely developed.

FIGURE 4.—Stages in the development of conidia of *Mastigosporium calvum* in pure culture on potato-dextrose agar at 40° F. × 1,075. (Diagramed from photomicrographs.)

On the host the development of the conidia (fig. 5) is approximately the same as on media. The spores are borne on short conidiophores which emerge directly from the leaf tissue, usually between the epidermal cells or through stomata. Stromatic development is moderate to slight, the fungus developing between the epidermal cells or in the cells.

Conidia usually are produced in relatively moderate numbers, and if the lesions are small and immature, few if any spores develop. On some of the bentgrasses larger numbers of spores were found, but the conidia do not occur in masses as in *Fusarium* or *Septogloeum*. The conidia, in addition, are somewhat brittle, and one or more cells may collapse, particularly under desiccation. As indicated from germina-

tion trials, the conidia apparently are fitted for quick germination and are relatively short-lived. They germinate from the apical end, producing one or two stout germ tubes which soon branch repeatedly.

The appendages or cilia that occur on conidia of the type material of *Mastigosporium album*, and which are characteristic of the genus on a majority of the reported collections from Europe, are apical or subapical, hyaline, tentaclelike protuberances (fig. 1, *J–O*). They resemble, except that they are considerably narrower, the mycelia from germinating conidia of *M. calvum* seen on potato-dextrose agar at Corvallis. Since, however, their position, shape, and length are fairly constant, they appear to be normal outgrowths formed as the result of some physiologic reaction which is not understood at present. They are believed to represent further development of the apical portions of the conidia and probably are morphologically akin to arrested germ tubes. Saccardo was uncertain about their nature, as indicated from his remarks (*14*).

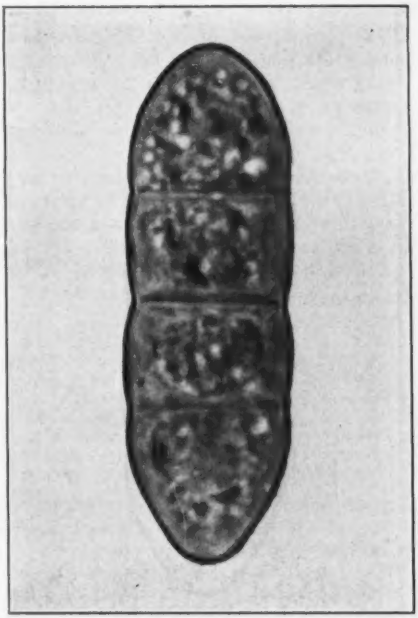

FIGURE 5.—Photomicrograph of conidium of *Mastigosporium calvum* on *Dactylis glomerata*, Corvallis, Oreg. × 2,000.

TAXONOMY

The appendaged *Mastigosporium album* and the nonappendaged *M. calvum* are distinct species if the present criteria for segregating species of fungi are logical. The two fungi are distinct because—

(1) The spores of *M. album* often have four cross walls, sometimes five; those of *M. calvum* have never more than three.

(2) The spores of *M. album* have appendages; those of *M. calvum* have not.

(3) The spores of *M. album* usually are longer and sometimes narrower than those of *M. calvum*.

(4) The two fungi maintain their respective characteristics in artificial culture on nutrient media.

(5) The host range of each fungus is fairly distinct.

A study of fresh material sent from Wales by Kathleen Sampson shows that the two fungi are, however, closely related. Both have coarse mycelia, which produce short, thick conidiophores. In their early stages the fungi appear almost identical, and until the tip of *Mastigosporium album* starts to elongate they appear to be the same species. *M. album*, however, grows from the apical end, producing the awl-shaped cell which frequently develops one or two cross walls in addition to the usual three cross walls in the main body of the spore. The apical cell then continues to elongate into the characteristic

appendage, which may become once, or more, forked. Additional appendages are sometimes formed from the side of the apical cell or cells. There is no question in the writer's mind that both fungi belong in the same genus and have arisen apparently from the same original species. The writer has considered the hypothesis that on certain hosts *M. album* produces appendages and on others not, and that this is a reaction to the host. From comparison with pure cultures this hypothesis appears unlikely. Therefore he proposes making two species in the genus *Mastigosporium*.

The genus *Mastigosporium* needs some revision to conform to the fungi included. It belongs in subsection Micromereae of section Hyalophragmeae of the Moniliaceae. This group includes among others *Fusoma* Corda and *Amastigosporium* Bond.-Mont. *Fusoma* has a very vague status as a fungus, with fusiform septate spores borne on scanty mycelia. Neither of the species of *Mastigosporium* appears to belong in *Fusoma*, although *F. rubricosa*, which is a synonym of *M. calvum*, has been described (*4*).

Amastigosporium graminicolum Bond.-Mont. (*1*) is the same as *M. calvum*. *Amastigis graminicola* Bond.-Mont. appears to be a simplified spelling of *Amastigosporium* attributed to Clements in Clements and Shear (*2*).

Mastigosporium is emended as follows:

Mastigosporium Riess (Emended).

Syn.: *Monothecium* Lib. in herb. and *Amastigosporium* (*Amastigis*) Bond.-Mont.

Mycelia in plants, epidermal and subepidermal, endophytic or somewhat ectophytic, septate, coarse, branched, hyaline; conidiophores, brief single or in small groups, short stipitate, continuous; conidia hyaline elliptical, large, navicular to subulate, formed by expansion of the hyphal tips, three-to-five septate, apical cells of conidia rounded and muticate, or awl-shaped and appendaged with simple or forked usually aseptate filiform appendages.

Included species, *Mastigosporium album* Riess (appendaged) and *M. calvum* (Ellis and Davis) comb. nov. (nonappendaged). Excluded, *M. lupini* (Sor.) Cav.

Mastigosporium lupini is excluded solely because of its pigmentation. Its manner of producing spores is remarkably like that of *M. album* and *M. calvum*.

Because it is virtually impossible to locate *Mastigosporium calvum* by use of present keys, it is suggested that future analytical keys to genera of fungi take cognizance of both the appendaged and nonappendaged species of *Mastigosporium*.

The data on spore size for available collections are presented in table 4. Apparently the two species are the same size until the elongation of the tip of *Mastigosporium album* starts. Most collections of the latter therefore average longer in mature spores than *M. calvum*.

In comparing the relatively fresh material from Wales with older exsiccati it appears that *Mastigosporium album* shrinks considerably after prolonged desiccation. The difference in width of the spores of the two species does not appear to be as great as indicated in table 4.

Mastigosporium calvum occurs on *Dactylis glomerata*, *Calamagrostis* spp., and *Agrostis* spp. Jaap (*8*) and Frank (*5*) report muticate spores of a *Mastigosporium* on *Alopecurus pratensis* which may be *M. calvum*. The fungus has not been found on *A. pratensis* in Oregon, although *M. calvum* occurs on *Dactylis* within short distances of small plots of *A. pratensis* on the experiment station farms at Corvallis and Astoria (table 1).

TABLE 4.—*Host, exsiccati number, ciliation (+ or −), location, conidial size, etc., of Mastigosporium album and M. calvum on grasses in Europe and North America*

Fungus	Host	Exsiccati, authority, or literature citation	Ciliation, verified by examination of exsiccati	Geographic location	Size of conidia	Appendages
M. album	*Alopecurus pratensis* L.	Riess (*6, p. 56*)	(1)		55 × 12 μ	+
	Deschampsia caespitosa (L.) Beauv.	De Thümen, Myc. Univ., 1872	+	Belgium	45–55 × 9–12	+
	A. pratensis L.	Sydow, Myc. Ger., 542	+	Germany	43–49 × 8–13	+
	do	Buch. et Bond. Fungi Ross. Exs., Ser. A, 197.	+	Union of Soviet Socialist Republics.	50–51 × 11–13	+
	do	Linhart, Fungi Hungar., 96	+	Hungary	50–55 × 13	+
	do	Krieger, Fungi Sax., 790 A and B	+	Germany	43–50 × 9–14	+
	do	Kabát et Bubák, Fungi Imp. Exs., 386	+	Bohemia	38–51 × 10–11	+
	do	Schroeter	−	Germany	48–55 × 11–13	+
	do	K. Sampson (Oreg. 8248)	+	Wales	31–53 × 12–16	+
Range of conidial size					31–55 × 8–16	
M. calvum	*Agrostis alba* L.	Oregon 10586	+	Oregon	32–51 × 12–16	−
	do	Oregon 8268	+	do	39–47 × 13–17	−
	A. palustris Huds.	Oregon 10308	+	do	29–38 × 10–15	−
	do	Oregon 8246	+	do	40–46 × 14–16	−
	A. tenuis Sibth.	Oregon 10585	+	do	35–45 × 11–16	−
	do	Oregon 10584	+	do	36–38 × 11–13	−
	A. verticillata Vill.	Oregon 8262	+	do	38–45 × 13–16	−
	Calamagrostis canadensis (Michx.) Beauv.	Herb., J. J. Davis	+	Wisconsin	40–45 × 11.5–12	−
	do	Univ. Toronto, Crypt. Herb., 1292	+	Ontario	33–40 × 11–14	−
	C. canadensis var. *scabra* (Presl) Hitchc.	Fungi Columb., 5019	+	Montana	37–44 × 10.7–14	−
	C. epigeios (L.) Roth	Sydow, Myc. Ger., 640	+	Germany	40–50 × 14–16	−
	C. halleriana	Krieger, Fungi Sax., 791	+	do	35–42 × 11–12	−
	Dactylis glomerata L.	Saccardo (*14*)	−	France	30–32 × 11	−
	do	Wakefield (*16, p. 253*)	−	England	32–38 × 10–12	−
	do	Oregon 10583	+	Oregon	40–45 × 13–15	−
	do	Oregon 10044	+	do	30–41 × 12–14	−
	do	Oregon 10011	+	do	34–38 × 10–12	−
	do	Oregon 10094	+	do	30–39 × 11–13	−
	do	Oregon 10203	+	do	31–37 × 10–12	−
	do	Oregon 10322	+	do	34–37 × 9–12	−
	do	Krieger, Schol. Pilze, 192	+	Germany	32–36 × 11–12	−
	do	Krieger, Fungi Sax., 792	+	do	35–40 × 12–14	−
	do	Bondarzeva-Monteverde (*1*)	−	Union of Soviet Socialist Republics.	40–60 × 14–16	−
Range of conidial size					29–60 × 9–17	

[1] Illustrations showed ciliated spores.

The earliest, although brief, description of *Mastigosporium calvum* appears to be that of *M. album* var. *calvum* Ellis and Davis (*3*). The combination *M. calvum* (Ellis and Davis) comb. nov. is proposed and the following synonymy listed:

Mastigosporium calvum (Ellis and Davis) comb. nov.

Syn.: *M. album* var. *calvum* Ellis and Davis, 1903.
M. album var. *muticum* Sacc., 1911.
Fusoma rubricosa Dearn. and Barth., 1917.
Amastigosporium graminicola Bond.-Mont., 1921.
Amastigis graminicola Bond.-Mont. (Clements), 1931.

Excluded, *M. album* var. *athrix* Eriks.

Wollenweber proposed *Bactridium triseptatum* (Sacc.) Wr. in his illustrated card index (*17*). His illustration 457 is based on Jaap's Fungi Rel. Exs. 494 and is typical for *Mastigosporium calvum* on *Calamagrostis*. His illustration 458, however, shows a typical species of *Bactridium* (*B. gymnosporangii* (Jaap) Wr.) that has distinct, somewhat elongated conidiophores arising from a small but definite sporodochial pad. *M. calvum* can scarcely be placed under *Bactridium*. To have placed this fungus under the combination *B. triseptatum*, Wollenweber must have seen the type of *Fusoma triseptatum* Sacc. If this material were *M. calvum*, Saccardo may have fallen into a trap, because his description and his illustration (*12*) and those of the apparently identical species *F. biseptatum* Sacc. (*13, p. 69*) are apparently those of a very much smaller-spored fungus referable to *Septogloeum oxysporum* Bomm., Rouss., and Sacc. Saccardo names his fungus *F. triseptatum* and then lists it as two-septate, while *M. calvum* is triseptate. His later description of *F. biseptatum* is singularly like his earlier one of *F. triseptatum*. It is possible that both *M. calvum* and *S. oxysporum* occur in the type of *F. triseptatum*. However, the published description is the final criterion; and *M. calvum* cannot possibly be referred to *F. triseptatum*.

Mastigosporium album var. *athrix* Eriks. is a *Septogloeum* and should be known as *S. athrix* (Eriks.) comb. nov. (fig. 1, *P*). It is highly probable that it may be the same as *S. oxysporum*.

The writer has found no evidence that *Mastigosporium calvum* is connected with *Dilophospora alopecuri*. In Oregon material of *D. alopecuri* on *Holcus lanatus*, it certainly does not appear to be connected with *M. album*. *M. album* has not been found in Oregon, and Miss Sampson's pure culture of it appears to be entirely different from a pure culture of the race of *D. alopecuri* on *H. lanatus*.

SUMMARY

Mastigosporium calvum (Ellis and Davis) comb. nov. causes a purple flecking and a leaf spot on *Dactylis glomerata* and an eyespot on the leaves of several species of *Agrostis* in northwestern Oregon. The fungus is a destructive parasite on these grasses during mild, rainy weather in winter and spring. It occurs on *Calamagrostis* spp. in Wisconsin. It also occurs on these grasses in Europe. It has been considered a variety of *M. album* Riess, which differs from it in having hyaline apical appendages, whereas *M. calvum* is muticate. *M. album*, which is common on *Alopecurus pratensis* and *Deschampsia caespitosa* in Europe, has not been reported from North America.

The genus *Mastigosporium* is emended to include elliptical, three- to five-septate, hyaline conidia borne on short, stipitate conidiophores. The apex of the conidia may have appendages (*M. album*) or may not have appendages (*M. calvum*).

No evidence was obtained that *Mastigosporium album* Riess is related to *Dilophospora alopecuri* (Fries) Fries.

Mastigosporium album var. *athrix* Eriks. is assigned to *Septogloeum athrix* (Eriks.) comb. nov., and its possible relation to *S. oxysporum* is mentioned.

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PRELIMINARY BIOCHEMICAL STUDIES ON EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON DEVELOPMENT AND COMPOSITION OF THE PEANUT[1]

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INTRODUCTION

The peanut (*Arachis hypogaea* L.) is one of the important crops grown in the southern part of the United States. About 2,000,000 acres of land are devoted to the crop in this country, producing about a million tons of unshelled[3] peanuts annually (*16, p. 572*).[4] In times of normal prices, the annual crop has a farm value of about $25,000,000.

The plant is of relatively great importance as a cash crop grown for the manufacture of oil, peanut butter, confectionery, salted peanuts, and stock feeds, and it is extensively grown for stock feeding on the farm (*2, p. 26; 17, p. 7*). Despite its importance, the peanut has had comparatively little careful study from the biochemical standpoint, except with reference to the properties of its oil and certain proteins. There are numerous growth and production problems that have important relationships not only to yields of unshelled peanuts per acre but also to filling of pods, quality of kernels, and adaptation of different types and varieties to specific regions or other conditions of culture.

Prior to the completion of the original draft of this paper the author found no literature on the physiological and biochemical behavior of the peanut with reference to the normal or desirable and abnormal or undesirable results often obtained under field conditions. Since then a report of studies of nutritional levels in the peanut plant by Moore (*11*) has appeared. Moore, working at Chicago, Ill., grew peanut plants in the greenhouse, in pots of quartz sand, with a series of nutrient solutions designed to produce wide differences in vegetative and reproductive behavior. Different fractions of the plants and fruits were analyzed for various forms of carbohydrate and nitrogenous substances. In general, the nutritional conditions resulted in unfruitfulness, offering no basis for comparison with the present studies. However, one comparison of high versus very low nitrogen supply showed for both shells and seeds a lower total sugar, lower total carbohydrate, and higher total nitrogen content. Data on plant size and yields and character of fruits were lacking, precluding comparisons with results of the present paper.

[1] Received for publication November 29, 1937; issued August 1938.

[2] The peanut samples were obtained from certain variety and fertilizer plots of the Virginia Agricultural Experiment Substation at Holland, Va., through the courtesy of that institution. Samples 5 and 6 were obtained from the plots of a preliminary spraying investigation being conducted cooperatively by the Virginia Agricultural Experiment Station and the Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, in which workers in the Division of Fruit and Vegetable Crops and Diseases are cooperating informally. The author acknowledges the kindness of these workers in making this material available.

[3] The word "unshelled" refers to peanuts in the shell throughout this paper.

[4] Italic numbers in parentheses refer to Literature Cited, p. 310.

The large-seeded Virginia type of peanut is apparently adapted to a very restricted range, which comprises an area about 50 to 60 miles in radius in southeastern Virginia and northeastern North Carolina and a smaller district in central Tennessee. The Spanish type of peanut, on the other hand, is generally well established throughout the southeastern quarter of the United States. The reasons for these very marked differences in adaptability are not at all understood.

A common cause of low yields of cleaned unshelled peanuts per acre and of low ratios of shelled to unshelled peanuts is the formation of many pods that contain poorly developed or quite undeveloped seeds. Varieties are known to differ in the extent to which they show this trouble, and the same variety may show widely differing degrees of it in various fields, years, or regions. It is not known to what extent light, temperature, moisture, mineral nutrients, soil texture, or cultural methods, either alone or together in various combinations, affect the development of plants and fruits in the regions where the crop is commonly grown.

The average yields and the efficiency of crop production in general are so far below the apparent possibilities that there is a pressing need for exhaustive fundamental studies of the plant in all stages of development and from numerous points of view—anatomical, morphological, and genetic, as well as biochemical and biophysical.

Certain cultural studies and seed-stock-improvement work on peanuts have been in progress for several years in the United States Department of Agriculture and have yielded results of definite value, and recently the Division of Fruit and Vegetable Crops and Diseases of the Bureau of Plant Industry has initiated studies of a more technical nature designed to solve some of these more fundamental problems.

The present paper reports the results of chemical examination of kernels and shells from six preliminary lots of peanut plants, which varied markedly in yield and appearance and which grew on soils of different texture or received different fertilizer or other chemical treatment. The object of this preliminary examination was to determine whether markedly different development and yield responses were accompanied by marked and easily determinable differences in physiological condition as revealed by estimation of certain chemical constituents of the fruits. These studies will be extended to other portions of the plant, and samples will be studied from a wide variety of natural field and controlled experimental conditions.

MATERIAL AND METHODS

EXPERIMENTAL PLOTS

The data concerning the fertilizer treatments of the experimental plots at Holland, Va., the peanut strains grown, etc., can readily be seen by reference to table 1, which shows that the yields varied markedly between varieties and treatments, but the yields per plant shown cannot be taken as typical of the response of entire plots receiving the respective treatments. In some instances the samples were selected from spots in the large plots in order to obtain varying degrees of plant size and vigor, regardless of the behavior of the plot as a whole, or to examine varietal differences. Nevertheless, the treatments of the various plots are presented as being of some interest.

The apparent influence of bordeaux mixture treatment on the yield is interesting. The Jumbo Virginia Runner of plot 5, which received, in addition to 1 ton of lime, three bordeaux mixture applications, gave 173.1 g of peanuts per plant as compared with 94.5 g for plot 6, which received the same amount of lime but no bordeaux mixture treatment. It seems reasonable to attribute the difference in part to the stimulating effect of copper, as shown by the considerably more vigorous growth and deeper green color of the plants in plot 5 as compared with those in plot 6.

TABLE 1.—*Type of soil, treatment, peanut varieties grown, and yields obtained from the various plots, 1934*

Plot No.	Type of soil	Treatment [1]	Variety	Plants taken for analysis	Average weight of unshelled peanuts per plant	Mean weight of peanuts per pod	Relative weight of shelled peanuts
				Number	*Grams*	*Grams*	*Percent*
1	Onslow fine sandy loam of lighter texture.	300 pounds of gypsum applied Aug. 1, 1933.	Small Virginia Runner.	20	105.0	0.93	66.0
2	do	300 pounds of gypsum applied Aug. 1, 1933, followed by 40 pounds of K_2O from kainite at planting.	Jumbo Virginia Runner.	50	40.8	1.48	67.0
3	Onslow fine sandy loam. Low spot of heavy texture.	300 pounds of gypsum applied Aug. 1, 1933, followed by 143 pounds of cottonseed meal at planting.	do	40	58.6	1.55	67.0
4	Onslow fine sandy loam of lighter texture.	300 pounds of gypsum applied Aug. 1, 1933 (check).	do	34	65.6	1.18	63.7
5	Onslow fine sandy loam of heavier texture.	1 ton of ground oystershell lime applied Apr. 1, 1934, followed by 3 bordeaux mixture applications (4–4–50) on July 15, Aug. 1 and 15, 1934.	do	13	173.1	1.38	65.5
6	do	1 ton of ground oystershell lime applied Apr. 1, 1934, but not treated with bordeaux mixture (check).	do	20	94.5	1.38	67.5

[1] Peanuts designated in pounds represent rates per acre.

PRESERVATION OF SAMPLES

The peanuts were picked in the field, put in paper bags, and within 6 to 7 hours were placed on a screen, shaken to free them from adhering soil, weighed, and transferred immediately to a forced-draft drying oven, where a temperature of 65° to 70° C. was maintained for about 20 hours. The moisture estimations of the fresh peanuts were not considered reliable enough to be recorded, because the plants had been pulled from the soil and exposed to an undetermined degree of drying for some hours before samples were taken. After the preliminary drying, the carefully cleaned peanuts were shelled and the kernels and shells ground separately in an electrically driven mill. The shells were passed through a 40-mesh sieve, but the kernels could not be so sifted because they had been ground somewhat coarsely to prevent any oil from being squeezed out. Since ground kernels at room temperature are known to become rancid and perhaps to undergo other changes with time, the samples were kept at about 2° until analyses were completed. Since the minced materials were placed

in tightly covered jars immediately after being ground and before their moisture content had reached equilibrium with that of the surrounding air, accurate moisture determinations were made in duplicate at the beginning and toward the conclusion of the investigation to ascertain whether the moisture content had changed during the time of making the analyses and, if so, to what extent.

Table 2 shows that when the dry-matter estimations made in October 1934 are compared with those of June 1935 the greatest difference is 0.32 percent in the case of the kernels (plot 1) and 0.55 percent for the shells (plot 2). It therefore appeared perfectly safe to calculate the results of the estimations of ash, oil, sugars, protein, etc., on the basis of dry matter found in October 1934. It is of interest to note that, after the unshelled peanuts had been dried at 65° to 70° C. for 20 hours, the separated kernels and shells from the various plots showed very similar percentages of dry matter, respectively, and with but one exception differed by only a few tenths of 1 percent.

TABLE 2.—*Percentage of moisture* [1] *in peanut samples preserved by drying at 65°–70° C. for 20 hours*

Plot No.	Moisture in—				Plot No.	Moisture in—			
	Kernels		Shells			Kernels		Shells	
	Immediately after preservation drying at 65°–70° C. in October 1934	After storing for 8 months at 2° C. in closed jars	Immediately after preservation drying at 65°–70° C. in October 1934	After storing for 8 months at 2° C. in closed jars		Immediately after preservation drying at 65°–70° C. in October 1934	After storing for 8 months at 2° C. in closed jars	Immediately after preservation drying at 65°–70° C. in October 1934	After storing for 8 months at 2° C. in closed jars
	Percent	*Percent*	*Percent*	*Percent*		*Percent*	*Percent*	*Percent*	*Percent*
1	3.33	3.65	4.06	3.54	4	3.25	3.23	3.70	3.53
2	2.95	3.22	4.26	3.71	5	3.27	3.00	3.79	3.37
3	3.10	3.34	3.56	3.23	6	3.48	3.52	4.42	4.39

[1] Moisture was determined at 105° C. just after initial drying and after 8 months' storage in closed containers at 2° C.

CHEMICAL ANALYSES

ASH CONTENT

In order to obtain uniform, strictly comparable ash determinations, duplicate portions from the six samples were incinerated simultaneously in an electric muffle furnace at a red heat below the fusion point of the ash. In each case a loose, homogeneous ash was obtained. The average percentages found are presented in table 3.

As will be seen, the kernels from the several plots showed considerable differences in the percentages of ash, which ranged from 2.22 for plot 5, with maximum growth and yield, to 2.56 for plot 2, with least growth and yield. For the shells, the lowest ash content was 2.73 percent for plot 3 (heavy soil high in organic matter) and the highest 4.04 percent again for plot 2. The variety of peanut, as well as the type of soil and the fertilizers applied, may have been a factor. The ash content of the shells was considerably larger than that of the corresponding kernels from each of the plots, the average ash content of the shells for all six plots being about 38 percent higher than that of the kernels.

TABLE 3.—*Percentage of total ash in peanut kernels and shells, determined on moisture-free basis*

Plot No.	Variety	Type of soil	Treatment [1]	Ash from—	
				Kernels	Shells
				Percent	*Percent*
1	Small Virginia Runner.	Onslow fine sandy loam of lighter texture.	300 pounds of gypsum applied Aug. 1, 1933.	2.37	2.78
2	Jumbo Virginia Runner.	do	300 pounds of gypsum applied Aug. 1, 1933, followed by 40 pounds of K_2O from kainite at planting.	2.56	4.04
3	do	Onslow fine sandy loam, low spot of heavy texture.	300 pounds of gypsum applied Aug. 1, 1933, followed by 143 pounds of cottonseed meal at planting.	2.31	2.73
4	do	Onslow fine sandy loam of lighter texture.	300 pounds of gypsum applied Aug. 1, 1933 (check).	2.41	3.35
5	do	Onslow fine sandy loam of heavier texture.	1 ton of ground oystershell lime applied Apr. 1, 1934, followed by 3 bordeaux applications on July 15, Aug. 1 and 15, 1934.	2.22	2.89
6	do	do	1 ton of ground oystershell lime applied Apr. 1, 1934 (check).	2.46	4.00

[1] Amounts designated in pounds represent rates per acre.

Because of the comparatively small quantities of ash obtained from the peanuts of each individual plot, the ash portions from all plots were combined and mixed for qualitative examination, the results of which are recorded in table 4.

TABLE 4.—*Qualitative examination of ash from peanut kernels and shells*

Cation or anion	Relative amount in—	
	Kernels	Shells
Cation:		
Potassium	Very much	Much.
Sodium	Very little	Very little (trace).
Magnesium	Considerable quantity	Present.
Calcium	Present in smaller quantity than magnesium.	Present; much more than in kernels.
Iron	Present	Do.
Aluminum	do	Present in greater quantity than iron.
Anion:		
Phosphate	Considerable quantity	Present; very much less than in kernels.
Sulphate	Present	Present; somewhat more than chlorine.
Silicate	Not present	Present in considerable quantity.
Chlorine	Present	Present (trace).

It will be seen that calcium occurs in the shells in considerably greater quantity than in the kernels and that silicon is present in the shells only. On the other hand, there is more potassium, magnesium, and phosphorus in the seeds than in the shells.

ETHER EXTRACT

Duplicate 10-g portions of ground peanut kernels and shells, after being dried at 100° C., were extracted with anhydrous ether in a Soxhlet extraction apparatus for 5 to 6 hours, the results thus obtained being designated as analyses A (table 5). The residue was then dried, taken out of thimbles, reduced to a fine powder, returned to the thimbles, and extracted for 5 more hours. This was done in the case of the kernels because originally they had been ground somewhat

coarse. For uniformity in procedure the shells were also extracted in two stages, though the material was fine and did not need to be ground again. The results of the first and second extractions combined were designated as analyses B, table 5.

TABLE 5.—*Percentage of ether-soluble substances in peanut kernels and shells, determined on moisture-free basis*

Plot No.	Ether-soluble substances in—				Plot No.	Ether-soluble substances in—			
	Kernels		Shells			Kernels		Shells	
	Analyses A	Analyses B	Analyses A	Analyses B		Analyses A	Analyses B	Analyses A	Analyses B
	Percent	*Percent*	*Percent*	*Percent*		*Percent*	*Percent*	*Percent*	*Percent*
1	46.70	46.91	0.55	0.57	4	46.86	48.02	0.56	0.60
2	46.77	47.42	.59	.61	5	47.92	48.59	.32	.38
3	48.41	49.41	.47	.48	6	47.25	48.49	.57	.57

In the case of the kernels the differences between analyses A and analyses B were quite pronounced, ranging from 0.21 percent (plot 1) to 1.24 percent (plot 6). This shows that analyses A do not represent the total ether-extractable material present in the kernels. For this reason, only analyses B, which can be considered as correct, are to be accepted. For the shells, A and B agree closely, but in five of the six samples the second stage of the extraction removed a slight additional amount of ether-soluble substances. The percentage of ether-extractable substances of the kernels from plot 3 (heavy soil and high organic matter) appears definitely greater than those from the comparable plots 2 and 4, whereas the reverse is true of the ether-extractable substances of the shells, an observation that merits further study. It seems also an interesting fact that the percentage of ether-extractable substances of the shells from the very vigorous plants of the bordeaux-treated plot was quite low in comparison with the control.

TOTAL NITROGEN AND PROTEIN

The total nitrogen was estimated by Gunning's modification of the Kjeldahl method. These determinations are designated in table 6 as analyses A. To make certain whether nitrate nitrogen was present, the oxidation of the peanut materials was effected also in the presence of salicylic acid (1 g of salicylic acid to 30 cc of sulphuric acid) and sodium thiosulphate, according to the method of the Association of Official Agricultural Chemists (*1*, *p. 21*). These determinations are designated as analyses B.

The percentage of protein was computed by multiplying the percentage of nitrogen by the factor 5.5. This factor was used by Jones and Horn (*9*) because Johns and Jones (*6*, *7*, *8*) had shown that the peanut contains two dominant proteins, the globulins arachin and conarachin, which contain 18.29 percent of nitrogen and which make up more than four-fifths of the total nitrogen of the peanut. The factor 5.5 was likewise employed by Ritthausen (*12*). The results thus obtained (table 6) are only approximations of the true protein content, for almost certainly some nonprotein nitrogen was present.

TABLE 6.—*Percentage of total nitrogen and of calculated protein in peanut kernels and shells, determined on moisture-free basis*

Plot No.	Kernels			Shells		
	Nitrogen by Kjeldahl method, analyses A	Nitrogen by Kjeldahl method modified to include nitrates, analyses B	Protein, average of analyses (A and B) ×5.5	Nitrogen by Kjeldahl method, analyses A	Nitrogen by Kjeldahl method modified to include nitrates, analyses B	Protein, average of analyses (A and B) ×5.5
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
1	4.88	4.89	26.87	1.56	1.60	8.69
2	4.99	5.06	27.64	1.11	1.14	6.19
3	4.90	4.91	26.98	1.21	1.24	6.74
4	4.96	4.92	27.17	1.55	1.60	8.66
5	4.63	4.71	25.69	1.09	1.13	6.11
6	4.91	5.02	27.31	1.51	1.43	8.09

Table 6 shows that the total nitrogen as determined to include nitrates in the kernels (analyses B) is in general insignificantly higher than the corresponding Kjeldahl nitrogen values. This is true for the shells also, the average total nitrogen content, including nitrates, being only 0.8 and 1.5 percent higher than the corresponding Kjeldahl nitrogen values in the case of the kernels and the shells respectively. In other words, the amount of nitrates, if at all present in the kernel and the shell, is so small as to be negligible.

Among the samples of kernels and shells there were no very striking differences in nitrogen content that could be definitely associated with the environment or growth of the plant. It is suggestive, however, that both kernels and shells from plot 5 showed a distinctly lower nitrogen content than the corresponding samples from plot 6. Although less striking, the nitrogen content of kernels of samples from plot 3 tended to be low as compared with that for plots 2 and 4. The differences among the shell samples were greater than among the kernel samples both relatively and absolutely.

CRUDE FIBER

The method of determining the crude fiber was essentially that of the Association of Agricultural Chemists (*1, pp. 280–281*). The results obtained (table 7) show that the differences in the crude-fiber content of the kernels from plots 2 to 6 (Jumbo Virginia Runner) were rather insignificant and that the value for plot 5 was the lowest. The differences in the crude-fiber content of the shells were marked, the value for plot 3 (heavy soil, high organic matter) being the highest, and that for plot 5 (bordeaux-treated) the lowest.

TABLE 7.—*Percentage of crude fiber in peanut kernels and shells, determined on moisture-free basis*

Plot No.	Crude fiber in—		Plot No.	Crude fiber in—		Plot No.	Crude fiber in—	
	Kernels	Shells		Kernels	Shells		Kernels	Shells
	Percent	*Percent*		*Percent*	*Percent*		*Percent*	*Percent*
1	2.82	65.42	3	2.20	66.23	5	2.11	61.63
2	2.21	63.46	4	2.24	63.13	6	2.23	62.62

CARBOHYDRATES

A careful review of the literature failed to reveal any estimations of reducing sugars, sucrose, or starch in the peanut kernel. Instead, nitrogen-free extract is ordinarily given, which is tacitly assumed to comprise the carbohydrates. The nitrogen-free extract is obtained by subtracting from the dry matter the sum of protein, crude fiber, ether extract, and ash. This indirect method is very convenient, and therefore is generally used in reporting analyses of feedstuffs, although it naturally involves the errors incidental to the determination of the afore-mentioned constituents and gives no knowledge of the specific carbohydrates present. Direct determinations of certain of the various carbohydrates are therefore necessary in order better to understand the physiological conditions associated with various types of response of the various parts of the peanut plant. The methods employed were as follows: 2 g of ground peanut kernels, first freed from fat by treatment with ether, were extracted with 60-percent alcohol in a Soxhlet extraction apparatus; the extract was freed from alcohol, and the aqueous solution was then introduced into a 250-cc volumetric flask; 1 to 2 cc of neutral lead acetate was added, and the mixture was made up with water to 250 cc and filtered clear.

DETERMINATION OF REDUCING SUGARS

Briefly stated, a 100-cc portion of the clear filtrate was boiled with Bertrand's solution A (copper sulphate) and B (Rochelle salt) for 3 minutes. The cuprous oxide obtained, after being washed well with hot water was dissolved in Bertrand's solution C (ferric sulphate) and titrated with Bertrand's solution D (standard potassium permanganate), the results being calculated as glucose (*3*, *13*, *14*).

DETERMINATION OF TOTAL SUGARS

A 75-cc portion of the clear filtrate was inverted according to Herzfeld's method (*4*). The cooled hydrolysate was neutralized with sodium hydroxide solution and made up to 100 cc. This, divided into two 50-cc portions, was used for the estimation of total sugar according to Bertrand's method, the results being calculated as invert sugar.

CALCULATION OF SUCROSE

The proportion of sucrose was found by subtracting the percentage of reducing sugars from that of total sugars and multiplying the difference by the factor 0.95.

ESTIMATION OF ACID-HYDROLYZABLE POLYSACCHARIDES

The estimation of the acid-hydrolyzable polysaccharides was made according to the method as outlined by Schmidt (*15*, *p. 924*), Lohrisch (*10*, *p. 375*), and Zemplén (*18*). The residue that remained after 2 g of peanut kernels had been extracted with ether and with 60-percent alcohol was hydrolyzed with a 2.1-percent hydrochloric acid solution for 2 hours. The cooled hydrolysate, after being neutralized with sodium hydroxide solution, was made up with water to 250 cc and filtered clear. Of this solution, 10-cc portions were used for deter-

mining the glucose according to Bertrand's method, the acid-hydrolyzable polysaccharides being calculated as starch by multiplying the glucose value obtained by the factor 0.9. For the details concerning the estimation of reducing sugars, sucrose, and hydrolyzable polysaccharides, the reader is referred to a previous publication (*5, pp. 716, 718*). The data secured are summarized in table 8.

TABLE 8.—*Percentages of reducing sugars, sucrose, and starch in the peanut kernel, determined on moisture-free basis*

Plot No.	Reducing sugars	Sucrose	Hydrolyzable polysaccharides	Total carbohydrates	Plot No.	Reducing sugars	Sucrose	Hydrolyzable polysaccharides	Total carbohydrates
	Percent	*Percent*	*Percent*	*Percent*		*Percent*	*Percent*	*Percent*	*Percent*
1	0.25	2.45	6.98	9.68	4	0.26	2.67	5.35	8.28
2	.26	3.05	5.22	8.53	5	.27	3.18	5.70	9.15
3	.22	2.87	4.88	7.97	6	.28	3.05	4.78	8.11

Table 8 shows that the percentage of reducing sugars is very small. On the other hand, the proportions of sucrose are quite noticeable. Still larger are the proportions of hydrolyzable polysaccharides, and the percentages of the total carbohydrates range from 7.97 (plot 3) to 9.68 (plot 1). These values indicate that because of the vigorous vegetative growth of the plants in plot 3, on a heavier soil high in organic matter, the maturity of the kernels was retarded. As a consequence, the percentage of hydrolyzable polysaccharides (4.88) and of total carbohydrates (7.97) was noticeably smaller than in the comparable plots 2 and 4, which showed, respectively, a starch percentage of 5.22 and 5.35, and a total carbohydrate percentage of 8.53 and 8.28. The bordeaux-sprayed plants of plot 5, which exhibited a leaf color and leaf area far superior to the unsprayed plants of plot 6, also showed a higher content of sucrose and hydrolyzable polysaccharides—in fact, the highest of any plot of the Jumbo Virginia Runner. It is also noteworthy that the kernels of the Small Virginia Runner (plot 1) displayed the highest percentage of hydrolyzable polysaccharides (6.98) and of total carbohydrates (9.68), doubtless owing largely to the variety.

SUMMARY

Six samples of peanut fruits involving two varieties were taken from areas and soil-treatment plots of an experimental field showing marked differences in growth, yield, and character of fruits. These were subjected to partial chemical analysis to determine whether easily recognizable differences in composition might be associated with environment and growth response.

The two varieties showed slight differences in ash, oil, protein, crude fiber, and carbohydrate content, but too few samples were involved to permit the drawing of any definite conclusions.

Ash content appeared to be decreased in both kernels and shells by a high nitrogen supply of the soil or by bordeaux mixture treatment that resulted in markedly increased plant growth and yield of pods.

Relatively unimportant differences in ether extract of kernels were observed among the samples, although in the shells the percentage

of ether-extractable substances was apparently decreased by high nitrogen or by the bordeaux treatment.

The total nitrogen content of kernels and shells apparently was not influenced by a high nitrogen condition of the soil due to application of cottonseed meal, but the nitrogen percentage was less in both kernels and shells from the bordeaux-treated plot.

Differences in crude fiber among the samples were very small and of doubtful importance.

Reducing-sugar content was extremely low in all samples of kernels. The sucrose content of kernels from the high-nitrogen plot treated with cottonseed meal and that for the bordeaux-treated plot were not materially different from their corresponding checks.

Total polysaccharides and total carbohydrates appeared to be decreased somewhat on the high-nitrogen plot and increased on the bordeaux-treated plot, in comparison with their respective checks.

This preliminary examination suggests that further biochemical and physiological studies may be expected to reveal important information on growth and development problems relating to yield and quality of peanuts.

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INFLORESCENCE BLIGHT OF THE DATE PALM[1]

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INTRODUCTION

In 1935 a blight of the inflorescence of the date palm in university date garden at Tempe, Ariz., was called to the attention of the senior author. The disease was present on the Sayer and Khadrawi varieties. In 1936 Khadrawi palms were not attacked, but the Khir variety, hitherto not observed to be affected, had flower clusters killed by the blight. A survey [2] of the palms showed the following blighted inflorescences, all pistillate:

Variety:	*Blighted inflorescences*
Iteema	1
Maktoom	2
Sayer (31 years old)	7
Sayer (31 years old)	5
Sayer (11 years old)	1
Khir (31 years old)	4

The occurrence of the blight in the date garden suggested the advisability of examining the date palms on the campus of the University of Arizona at Tucson. A survey of these palms showed the disease to be present on staminate inflorescences.

The date palms with which the writers worked in university date garden are chiefly known varieties imported from Africa and propagated by means of offshoots. The history of the garden is given in Arizona Agricultural Experiment Station Bulletin 149 (*1*).[3] Palms on the campus of the University of Arizona, which are mentioned in connection with the present study, are seedling in origin and nondescript in variety, and were planted primarily for ornamental purposes.

Until 1936 inflorescences infected with blight fungi had been found only on palms 30 to 31 years old, but during the flowering season of 1936 an inflorescence blighted on a palm only 11 years old. Most infected inflorescences in the date garden have been found on pistillate flowers, but blighted staminate inflorescences have also been collected there and on the university campus. Hilgeman [4] states that a blight which occurs generally on staminate flower clusters in the date garden and throughout the Salt River Valley in Arizona has been popularly attributed to *Thielaviopsis paradoxa* on the basis of work done on palms in California (*4*). The present work (the first investigation of inflorescence blight to be undertaken at this station) appears to indicate that more or less of the blight in Arizona date palm orchards is caused by fusaria.

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[1] Received for publication February 28, 1938; issued August 1938.
[2] This survey was made by Robert H. Hilgeman, assistant horticulturist.
[3] Italic numbers in parentheses refer to Literature Cited, p. 318.
[4] Personal communication.

SYMPTOMS

Initial infection of date inflorescences may occur anywhere on the rachis from the base to the branches, on the branches, or in the flowers. Primary infection of the rachis results in water soaking of the tissues and subsequent discoloration of the stalk, the color ranging from wood brown (*6*) to fawn to bone brown, with shrinking of the infected tissues (pl. 1, *A*, *a*). Disease of the branches, which are discolored like the rachis, results in the death of the flowers above the infected spot. Attacked flowers (pl. 1, *E*, *F*) are a discolored brown.

Stalks of pistillate inflorescences often are so weakened by infection that they break under the increasing weight of the fruit. The break across the stalk is at right angles to the axis, often resembles a cut made by a sharp instrument, and is deep enough to permit the distal part of the branch above the break to bend back against the basal part. Although this breaking of the stalk following infection is common, apparently sound stalks occasionally break. The writers have cultured some that gave no parasitic organisms.

CAUSE

Blighted parts of the date inflorescence, sometimes in the field and regularly in the laboratory when kept moist, become overgrown with a gray to buff mycelium, or with a covering of pale purplish to pale Congo pink filaments, or with a mycelium in which these colors are mixed. Blocks of tissues from infected parts, which were surface-sterilized and cultured on 2-percent potato-dextrose agar, steamed yellow corn meal, and steamed rice, yielded two species of *Fusarium* and one species of *Helminthosporium*. One *Fusarium*, in 10-day cultures on potato-dextrose agar, was a pale grayish vinaceous above and pale grayish vinaceous to brownish vinaceous in streaks below. On steamed rice in 6-day cultures it was light vinaceous gray above and light vinaceous lilac with rocellin purple lines around the lighter areas below.

The other species of *Fusarium*, in 2-day cultures on potato-dextrose agar, was sea-shell pink to salmon buff above, and gray to ochraceous orange (margin of colony to center) below; 10-day cultures on the same medium were pale ochraceous salmon to salmon buff above (the lighter color in the margin and between the concentric growth rings), and gray to orange below. On steamed rice, 9-week cultures were pinkish buff above and pinkish buff to hazel below. This species often gave concentric growth rings 2 to 4 mm wide on potato-dextrose

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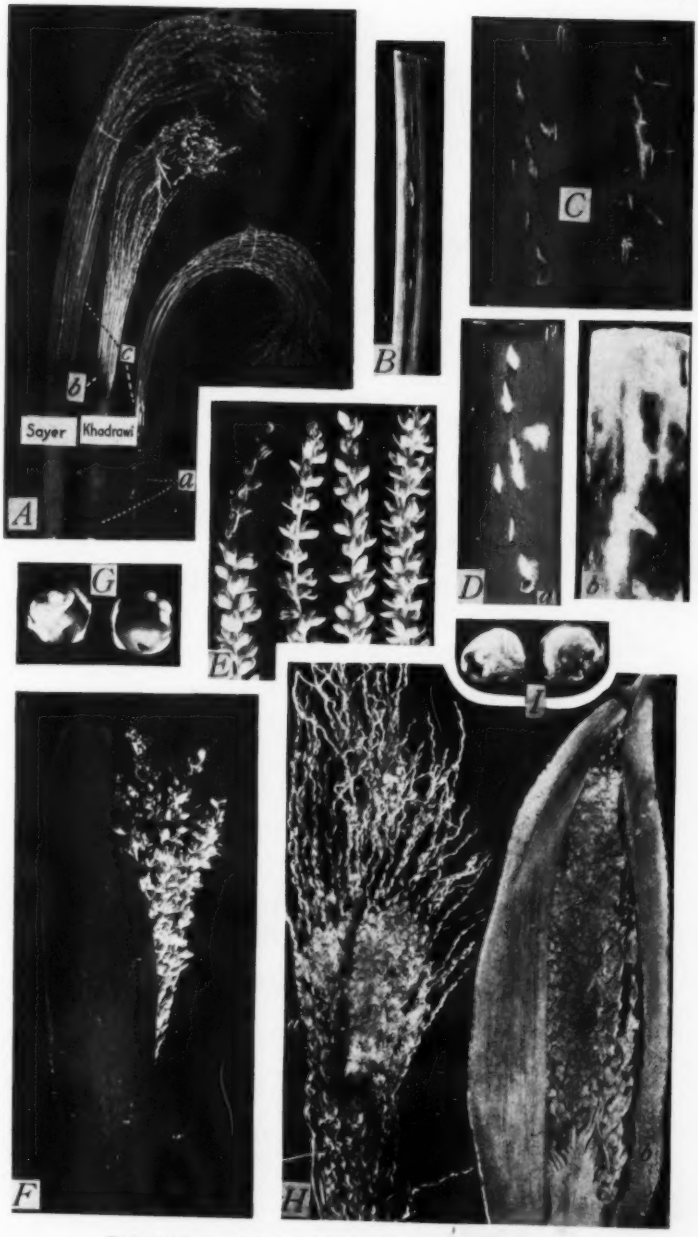
EXPLANATORY LEGEND FOR PLATE 1

A, Naturally blighted inflorescence of date palm, Khadrawi variety, with: *a*, Basal discoloration and shrinking of rachi; *b*, discoloration of branches; *c*, mycelium and spore masses of *Fusarium*. *B*, Piece of rachis inoculated in situ with *Fusarium moniliforme* on April 21, 1935, and photographed May 24, 1935. Discoloration of the rachis extends for a considerable distance above and below the points of inoculation. *C*, Pieces of rachis of date palm laboratory-inoculated with *F. moniliforme* April 21, 1935, and photographed May 4 following. *D*, Pieces of rachis laboratory-inoculated with *F. moniliforme* April 21, 1935, and photographed May 15: *a*, Piece incubated at 5° C.; *b*, piece incubated at room temperature. *E*, Flowers of seedling date palm inoculated with *F. moniliforme* April 21, 1935, and photographed May 4. *F*, Natural infection of the staminate inflorescence of seedling date palm with *F. moniliforme* May 24, 1935; terminal flowers discolored and killed. *G*, Green date fruits inoculated by spraying with a spore suspension of *F. moniliforme;* photographed 7 days after inoculation. *H*, Natural infection of staminate inflorescence of date palm with *F. semitectum* (*F. lateritium* var. *fructigenum*?), July 20, 1935: *a*, Late stage showing mycelium and spore masses on inflorescence in the university date orchard; *b*, early stage, campus, University of Arizona. *I*, Green date fruits inoculated by spraying with a spore suspension of *F. semitectum* (*F. lateritium* var. *fructigenum*?); photographed 7 days after inoculation.



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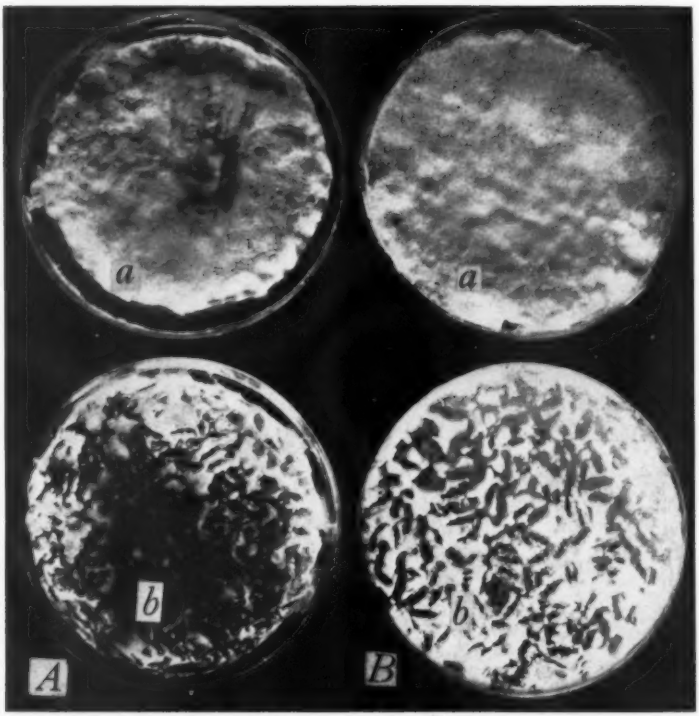


A, Culture of *Fusarium moniliforme* from blight of date inflorescence, on steamed rice 39 days at 28° C.: *a*, Upper surface, light vinaceous gray; *b*, lower surface light vinaceous lilac with rocellin purple borders around lighter areas. *B*, Culture of *Fusarium semitectum* (*F. lateritium* var. *fructigenum*?) from blight of date inflorescence, on steamed rice, 39 days at 28° C.: *a*, Upper surface, pale ochraceous salmon to salmon buff; *b*, lower surface gray to ochraceous orange.

agar. Plate 2, *A* and *B*, shows the appearance of older cultures of the two fusaria.

The vinaceous culture of *Fusarium* was identified by Dr. C. D. Sherbakoff, of the Tennessee Agricultural Experiment Station, as *Fusarium moniliforme* Sheld., which agreed with the report on the same fungus received from the Centraalbureau voor Schimmelcultures, Baarn, Netherlands. The buff culture was identified by Sherbakoff as *Fusarium semitectum* Berk. et Rav. and by the Centraalbureau as *Fusarium lateritium* Nees var. *fructigenum* (Fr.) Wr.

The species of *Helminthosporium* found by the junior author and by him proved capable of causing decay of the flower clusters of the date palm is not considered in the present paper.

INOCULATIONS

On April 19, 1935, three spadices of *Phoenix dactylifera L.*, whose spathes had been open a few days, were inoculated by spraying the exposed flowers with a heavy suspension of spores of *Fusarium moniliforme;* and a small hole was cut through an unopened bract of a fourth inflorescence into which a spore suspension of the fungus was injected, so that the spathe formed a natural moist chamber. On the same date four rachi were inoculated by inserting small pieces of a pure culture of the fungus from potato-dextrose agar into small incisions made with a sterile scalpel and afterward moistened with sterile distilled water. Both staminate and pistillate inflorescences were used in the inoculations. On May 4 many diseased flowers were evident in the inoculated clusters (pl. 1, *E*), but the controls were normal. A series of 12 isolations was made from the inoculations, and all but 1 culture gave the *Fusarium* species used in the inoculations of the inflorescences. Too rigorous surface sterilization of the tissues used in culture may account for the single failure.

Again on April 21, 10 rachi on 2 palms were wound-inoculated as previously described; 13 days later the inoculations had water-soaked margins and presented the appearance shown in plate 1, *C*, although the controls showed no infection. Pieces of the water-soaked tissues were surface-sterilized with a 1:1,000 mercuric chloride solution and cultured, with the recovery of *Fusarium moniliforme* in 11 of the 15 tubes.

Two large pieces of rachi, which were scalpel-inoculated with *Fusarium moniliforme* and placed under a bell jar in the incubator at 27° C., showed good fungus growth on the wounds in 3 days, although no growth occurred on control pieces similarly wounded but not inoculated. One piece was then transferred to the refrigerator and kept at a constant temperature of 5° in a similar moist chamber. At the end of 8 days the two pieces were photographed (pl. 1, D, *a* and *b*). Growth at the lower temperature was slight, but at the higher temperature it was luxuriant.

The piece of rachis from the incubator was afterward removed to a moist chamber in the laboratory and there it produced numerous perithecia. The perithecia were dark blue, ovoid, contained asci with eight ascospores arranged in two series, and agreed well with the measurements of perithecia, asci, and ascospores given by Wollenweber (7) for *Gibberella moniliformis* (Sh.) Wineland. Ascospores from the perithecia were cultured on malt agar from which transfers

were made to potato-dextrose agar; the resulting mycelial growth appeared to be identical with *Fusarium moniliforme* and produced similar microconidia.

On May 24 a rachis which had been inoculated with a culture of *Fusarium moniliforme* on April 21 was found to have a long, depressed, grooved lesion (pl. 1, *B*) which had resulted from the coalescence of the lesions initiated by inoculation. Blocks of the infected tissues from this piece of rachis were killed and sectioned for histological study.

On May 24 a natural infection of a staminate inflorescence was found on a date palm on the university campus. The spathe had been open for a few days only, yet the top of the flower cluster was very brown and the infection appeared to be progressing downward (pl. 1, *F*). From cultures of the infected flowers *Fusarium moniliforme* was isolated.

Inoculations of date palm parts with *Fusarium semitectum* (*F. lateritium* var. *fructigenum*, according to the Centraalbureau voor Schimmelcultures) were made as follows: Wound inoculations on five rachi and two petioles and spore-suspension sprayings on two inflorescences, all made on May 15 with proper controls. On June 15 lesions were present on all inoculated parts except the petioles, but none were present on controls; the lesions developed much more slowly than those caused by inoculation with *F. moniliforme*. From the inoculated tissues 20 cultures were made with surface-sterilized pieces; 12 of the cultures gave the *Fusarium* used in the inoculations—the only pathogene recovered. Green, surface-sterilized date fruits from palms on the campus, placed in Petri dishes, were vigorously attacked by *F. semitectum* (*F. lateritium*?) and by *F. moniliforme*, after being sprayed with spore suspensions of these species (pl. 1, *G*, *I*).

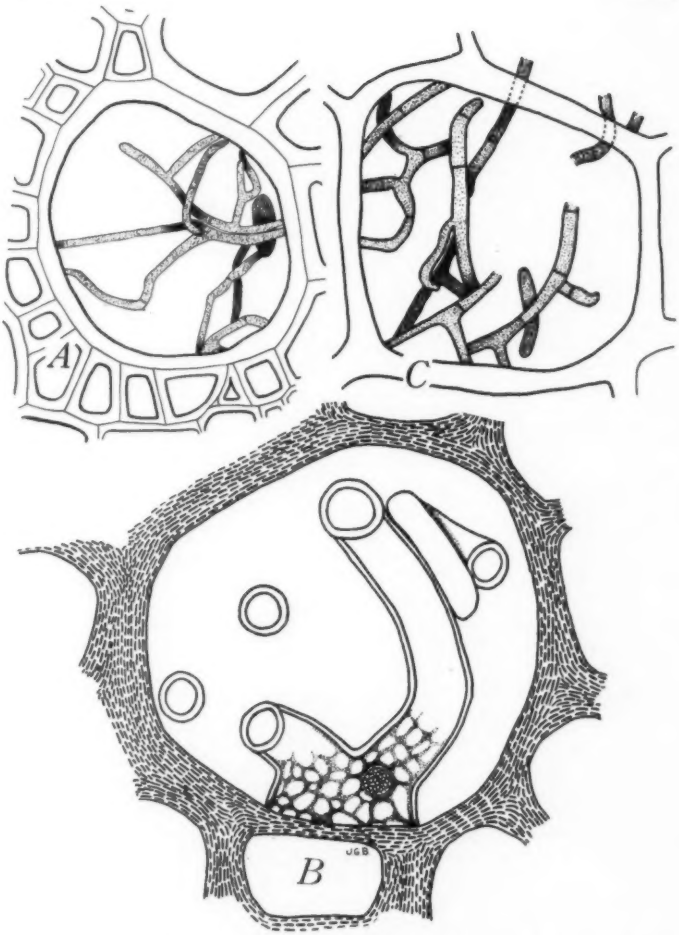
PATHOLOGIC HISTOLOGY

Preparations for microscopic investigation were made from the tissues of rachi and other parts infected with *Fusarium moniliforme*. The fungus infects both fibro-vascular bundles and parenchyma cells, which are more or less discolored as a result of invasion. In the bundles the filaments are located chiefly in the tracheae (pl. 3, *A* and *B*); in the parenchyma tissue they are both intercellular and intracellular (pl. 3, *C*). Infected parenchyma cells in slides stained with carbol fuchsin-light green (clove oil) acquired a deeper red than healthy cells in the same preparations. The vacuolar structure of the hyphae in the vessels was clearly evident under high magnification (pl. 3, *B*).

CONDITIONS AFFECTING THE BLIGHT

Although a study of the effect of environmental conditions on the prevalence of the blight of date inflorescences has not been made, observations indicate that the weather in the Salt River Valley during the flowering season is usually favorable for its development; hence the general occurrence of the disease. Viable cultures of *Fusarium* from old inflorescences show that the heat of summer, the dryness of autumn, and the cold of winter do not injure the fungus, which continues capable of producing abundant spores.

How the spores of the fusaria of inflorescence blight are disseminated remains to be determined. Insects are frequently very numerous in



A, Fusarium moniliforme: Parts of hyphae in trachea of fibrovascular bundle of rachis. × 621.4. *B,* vacuolate structure of a part of a hypha of *F. moniliforme* in a trachea of date rachis. × 2,571. *C,* parts of hyphae of *F. moniliforme* in a parenchyma cell of rachis of date palm. × 621.4.

the tops of date palms, especially during flowering and fruiting. Possibly they are the important agents of dissemination. The practice among date growers of carrying flower clusters from staminate palms into their exclusively pistillate plantings no doubt facilitates the spread of the inflorescence blight.

The effect of spraying on fusarium blight of date flower clusters has not been specifically investigated, although the trees in university date garden have been sprayed for several years in an effort to control fruit rot. In these sprayings copper acetate, lime-sulphur, and instant bordeaux mixture (4–4–50) have been used. Sprays for fruit rot usually have been applied later in the season than they should be to control inflorescence blight. Perhaps the first step in the control of the blight should be the removal of all staminate flower clusters after pollination is effected, and the removal of all pistillate rachi after the fruit is harvested. With these sources of infection out of the way, a thorough spraying of the palms before the spathes break open should go far toward eliminating the blight.

DISCUSSION

In some respects the blight of date inflorescences herein discussed is similar to the decay described by Cavara (*2*), and later by Chabrolin (*3*), under the name "Khamedj," for palms in north Africa. Both diseases are parasitic, both attack staminate and pistillate flower clusters and related parts, both originate externally, and both cause browning of the affected tissues. Also, the Khamedj parasite has been proved to attack uninjured tissues just as the fusaria in inflorescence blight attacked uninjured green date fruits. However, there should be no possibility of confusing the Khamedj parasite with the fusaria, for the former, *Mauginiella scaettae* (*2, 3*), belongs to a genus having affinity with *Septocylindrium* and *Geotrichum;* it produces a white efflorescence, becoming pulverulent over reddish spots which later become black; the external mycelium disappears from the infected spots; and conidia are borne in chains. Except for a somewhat pulverulent appearance, the fusaria differ from the Khamedj parasite as described, and no pathologist would have difficulty in distinguishing the parasites.

The blight described in this paper may be the same inflorescence decay mentioned by Fawcett and Klotz (*4*) in their bulletin on diseases of the date palm, although they do not give the species of *Fusarium* which they isolated in their studies. They state (*4, p. 23*): "*Fusarium* sp. is sometimes found mixed with either *Thielaviopsis* or *Diplodia*, or it may be alone." In another publication (*5, p. 157*) they say: "A species of Fusarium was later found as the primary cause of a decay of certain male inflorescences of the date palm." The fact that they obtained less injury from their inoculations with *Fusarium* species may have been due to their use of a different species from those employed by the writers, or to different environmental conditions. Inoculation with *Fusarium moniliforme* in the writers' experiments soon resulted in extensive decay. From brief description of the *Fusarium* rot given by the California investigators it is impossible to determine whether the inflorescence decay which they mention is identical with the blight observed in the Arizona plantings.

That the blight may affect the inflorescences of a comparatively wide range of varieties and ages of date palms is indicated by the list given in the introduction to this paper, and this probably means a spread of the disease unless steps are taken for its control. Persistent blighted flower and fruit clusters may easily become serious sources of infection from year to year. One suspicious case found on the campus strongly suggests this means of carry-over. A rotted cluster of flowers from the preceding year, within a partly opened spathe, was covered and interspersed with a powderly mass of *Fusarium* spores; on the same palm several blighted inflorescences were found near the old blighted flower cluster.

SUMMARY

An inflorescence blight attacks several varieties and ages of date palms in southern Arizona.

Primary infection results in water soaking and discoloration of the infected parts; flowers may be killed by direct attack or indirectly by the infection of parts below them; green fruits decay when sprayed with a spore suspension of either of the fungi concerned.

Two species of *Fusarium* cause the blight, working together or separately. One of these is *Fusarium moniliforme* Sheld.; the other is either *F. semitectum* Berk. et Rav., (as identified by Sherbakoff) or *F. lateritium* Nees var. *fructigenum* (Fr.) Wr. (as indicated by Centraalbureau voor Schimmelcultures).

The results of numerous inoculations with the two species of *Fusarium* on different parts of the date palm are given.

A brief description of the pathologic histology is presented.

Conditions affecting the blight are discussed, and suggestions for its control are given.

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U. S. GOVERNMENT PRINTING OFFICE: 1938